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Fossil Mammals of Africa

No. 11

ERINACEIDAE FROM THE MIOCENE OF EAST AFRICA

P. M. BUTLER

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(*Royal Holloway College, University of London*)

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56 [illegible]

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INTRODUCTION

At the present day the Erinaceidae are distributed through the Palaearctic, Oriental and Ethiopian regions. They are divided into two sub-families, the Echinosoricinae, confined to S.E. Asia, and the hedgehogs (Erinaceinae), which in Asia do not extend beyond northern China, the Indus basin and Madras (Ellerman & Morrison-Scott 1951). In Africa south of the Sahara the family is represented by species of *Atelerix* (including *Aethechinus*), regarded by Ellerman & Morrison-Scott as a subgenus of *Erinaceus*. There are no hedgehogs in Madagascar.

The fossil history of the group has been reviewed by Butler (1949). It had a wide distribution in Europe and Asia in the Oligocene, when the existing sub-families had already separated, and the range of the family extended to North America. Apart from a species of *Atelerix* (Broom 1937), no fossil erinaceids have hitherto been described from Africa. It is therefore of some interest that they have proved to be fairly common in the Miocene deposits of the Kavirondo Gulf area, on the north-eastern side of Lake Victoria. The deposits were described by Kent (1944) and Shackleton (1951), and an account of the history of the discovery of fossil mammals in the area was given by Le Gros Clark & Leakey (1951).

Five species of Erinaceidae are distinguished, of which four, comprising the great majority of specimens, are placed in the Erinaceinae, but the sub-family Echinosoricinae is represented by only two specimens. In the Miocene of Europe the two sub-families were of approximately equal importance. Of the four Erinaceinae, one is referred to the genus *Amphechinus* (=*Palaeoerinaceus*), which also occurs in Europe, but the African species possesses a number of more primitive characters and is not closely related to the only European species of which the skull is well known, the Aquitanian *A. edwardsi*. The remaining African hedgehogs are placed in a new genus, *Gymnurechinus*, which though closely related to *Amphechinus* shows some peculiar specializations, and at the same time is nearer than *Amphechinus* to *Erinaceus*. The Miocene erinaceid fauna of Africa is therefore distinct from that of Europe, and a direct faunal interchange between the two areas would seem to be improbable. Since Africa is believed to have been isolated during the Oligocene, when the Erinaceidae had a wide distribution in the Northern Hemisphere, it seems likely that the Miocene Erinaceidae of Africa were derived from a Eurasiatic source, and entered Africa, probably from Asia, when its isolation came to an end at the beginning of the Miocene. Unfortunately, fossil Erinaceidae are known in Asia only from Mongolia and northern China and these specimens are too fragmentary for reliable conclusions about their relationships to be drawn.

ACKNOWLEDGMENTS.—I am greatly indebted to Dr. L. S. B. Leakey for placing the material in my hands for study; to Dr. F. C. Fraser and Dr. T. C. S. Morrison-Scott, of the British Museum, and to the Abbé R. Lavocat of the Muséum National d'Histoire Naturelle, Paris, for access to comparative material; to Dr. R. M. C. Eagar, Mr. J. H. Halliday, Dr. W. D. Hincks, Mr. C. W. M. Pratt, Professor R. Warwick, Professor D. M. S. Watson, and particularly to Dr. A. T. Hopwood for useful suggestions and criticism; and to Mr. R. Newton for assistance in the preparation of photographs.

SYSTEMATIC DESCRIPTION

Sub-family ERINACEINAE

Genus *GYMNURECHINUS* nov.

DIAGNOSIS.—Erinaceinae which resemble *Amphechinus* Aymard in most features of the skull, but differ in that: (1) the anterior incisors are less enlarged and the root of I_2 terminates below P_2; (2) the molars are less reduced, and the cheek-teeth are situated so that P^4 is anterior to the orbit. P_2 has two roots. The fenestration of the palate is rudimentary; there is no basisphenoidal pit.

TYPE SPECIES.—*G. leakeyi* sp. nov.

Gymnurechinus leakeyi sp. nov.

(Plate 1, Pl. 2, figs. 12–16, Pl. 3, figs. 20–22, Pl. 4, figs. 33, 36, Text-figs. 1–7, 8*a*, 9*a,d*)

DIAGNOSIS.—Differs from other species in the genus in the broad sagittal crest, which is rectangular in cross-section, and in the relatively transverse M^1. Posterior lambdoid crest well developed, lambdoid area relatively large. Hypocone of P^4 normally developed. Width of palate across paracones of first molars 16·3–16·5 mm., alveolar length of M_{1-3} 10·0–10·8 mm.

The species is named after Dr. L. S. B. Leakey.

HOLOTYPE.—Rs 12.32,* a skull with associated lower jaw, in good condition except that the snout is broken off in front of the canines, the teeth are much worn, and the face shows slight lateral crushing and some weathering. It was found at Hiwegi (sub-site R 12), on the eastern side of Rusinga Island.

REFERRED MATERIAL.—33 specimens, all from Rusinga, may be referred to *G. leakeyi* with more or less confidence. This species is by far the commonest Insectivore in the Rusinga deposits, but it has not been found at Songhor. The referred specimens are listed below.

HIWEGI

Sub-site R 1.

402.50	Cranium showing the roof of the tympanic chamber.
1575.50	Isolated M^1, worn.
759.47	Fragment of maxilla with broken I^1. This seems to differ slightly from 491.51, and may not belong to this species.
1.32	Fragment of lower jaw with well-preserved P_4 and M_1. It agrees with 864.50 except that M_1 is a little larger.

---

* The catalogue numbers are those of the Coryndon Museum. Specimens are numbered according to their place of origin and the year of their discovery: thus Rs 12.32 is no. 12 in the Rusinga collection of 1932.

1a.32 Fragment of lower jaw with well-preserved P_4, which agrees with 864.50.

Sub-site R 1A.

202.47 Badly crushed facial part of skull.

828.47 Maxilla fragment containing P^3–M^2 in good condition. The teeth are a little larger than in the type.

Sub-site R 3.

1.49 Uncrushed skull from which the roof has been removed to show the brain-cast and the interior of the olfactory chamber. The tip of the snout is missing, but the specimen shows very well the nuchal crest, the external pterygoid process, the palate and some of the teeth.

491.51 Well-preserved anterior half of a skull with worn teeth. The palate and part of the cribriform plate are visible. There are associated parts of both halves of the lower jaw (separately numbered 504.51), the teeth of which fit the upper teeth of 491.51.

259.49 Crushed cranium.

1006.50 Associated M^1 and M^2, not quite so transverse as 828.47 or 1575.50.

864.50 Part of a lower jaw with well-preserved P_4–M_3.

1702.50 Fragment of lower jaw with weathered P_4 and M_1. The ramus is not so deep as in the holotype or 864.50.

Sub-site R 3A.

623.50 Anterior part of skull without teeth, showing the palate and part of the cribriform plate.

411.51 Anterior part of skull with P^2 and C. Differs from other specimens in the broader nasals.

587.50 Fragment of maxilla with moderately worn and weathered P^4 and M^1, agreeing closely with 864.50.

513.49 Fragment of lower jaw with P_4.

588.50 Fragment of lower jaw with alveoli of I_3–M_1. More slender than in the holotype or 864.50.

Sub-site R 12.

12a.32 Skull lacking the anterior end and the teeth, with well-exposed brain-cast.

WANYAMA

573.49 Fragment of mandible with worn M_1 and M_2, agreeing with 864.50.

KAMUNGERE

684.49 A badly crushed cranium, which appears to agree with the holotype.

KULU—WARENGU AREA

734.48 Skull, much weathered, with lower jaw and part of the atlas and axis vertebrae. It agrees closely with the holotype.

735.48 Jaw fragment with alveoli of molars.

KATHWANGA—KIAHERA AREA

Kathwanga.

671.48 Cranium, rather weathered.

1971.50 Anterior end of lower jaw with unworn P_2. The jaw is more slender than in the holotype, and agrees closely with 588.50.

1539.50 Jaw fragment with much weathered M_1, apparently a little larger than 864.50, but agreeing with 1.32.

698.48 Jaw fragment with alveoli of M_1–M_3. It is rather slender, and its identity is not certain.

Sub-site R 106.

930.50 Jaw fragment with the roots of I_3–P_4, much like 1971.50 but rather deeper.

855.48 Jaw fragment with worn and broken P_4.

553.47 Jaw fragment with P_4.

290.49 Jaw fragment with alveoli of M_1–M_3, agreeing in size with the holotype.

Sub-site R 111.

111.32 Skull with upper cheek-teeth. Agrees closely with the holotype.

RUSINGA, SITE UNKNOWN

32.32 Cranium showing part of brain-cast.

THE SKULL.—The skull is smaller than in most of the Recent Erinaceinae; in width it agrees best with large specimens of *Atelerix albiventris*, but it is relatively longer. It is somewhat larger than that of *Amphechinus edwardsi* (Filhol), and the measurements agree closely with those of the nearly complete specimen of *Neurogymnurus cayluxi* Filhol (holotype of *Cayluxotherium elegans* Filhol) in the Paris Museum, figured by Friant (1934*a*). The referred specimens indicate that there was only slight variation in size (Table 2).

The greater length of the skull in comparison with Recent Erinaceinae is shown mainly in the snout and the postglenoid region (Table 1). In the length of its snout *Gymnurechinus* is comparable with *Amphechinus* and *Neurogymnurus*. In the length of the mid-cranial region, between the palatal crest and the eustachian foramen, it resembles *Neurogymnurus* and the Recent Erinaceinae, and exceeds *Amphechinus*, in which this part of the skull is abbreviated. The skull is relatively higher at the posterior end than in the Recent Erinaceinae, but agrees in this respect with *Amphechinus*.

FACIAL REGION.—The nasals are narrow with nearly parallel sides. They reach the level of the postorbital processes, and thus extend farther back than in *Amphechinus* and the Recent Erinaceinae, but not so far as in *Proterix*. In *Neurogymnurus*, from Filhol's figure (1880), the nasals terminate above the lachrymal foramina; they are still shorter in Recent Echinosoricinae. Rs 411.51 is abnormal in that its nasals are wider near the posterior end of the premaxilla.

The premaxillary portion of the snout is seen best in Rs 491.51 (Plate **2**, figs. 12 & 14). The premaxilla does not contribute to the length of the snout as much as in *Amphechinus*: the ratio, alveolar length of premaxilla/width across the canines is

0·90 in *Amphechinus edwardsi* (from Viret, 1938, fig. 6), 0·62 in *Gymnurechinus leakeyi* (estimated), and 0·61 in *Erinaceus europaeus*. The narial opening is narrower in *Gymnurechinus* than in *Erinaceus*, but corresponds in shape to that of *Hemiechinus auritus*. The extranasal process of the premaxilla meets the frontal above the infraorbital foramen, as in *Amphechinus*; this contact is frequently absent in Recent Erinaceinae.

The maxilla extends dorsally over the anterior part of the orbit and is indistinguishably united with the lachrymal as in other adult Erinaceidae. Dorsal to the orbit there is a well-marked concavity for the origin of the levator muscle of the snout. There is a well-developed pre-lachrymal flange, so that the lachrymal foramen opens inside the orbit. The root of the zygoma is hollowed out for the origin of snout muscles. These are primitive features found in *Neurogymnurus*, the Echinosoricinae and *Amphechinus*, but to a large extent lost in Recent Erinaceinae.

P^4 is anterior to the orbit; the infraorbital foramen opens immediately anterior to the roots of P^4; the zygomatic process arises opposite the posterior part of M^1 and the anterior half of M^2. In these relations of the teeth to the skull *Gymnurechinus* resembles *Neurogymnurus*, *Galerix* and the Recent Erinaceinae, but differs from *Amphechinus*, in which the teeth are situated farther back so that P^4 is below the orbit, the infraorbital foramen is above the middle of P^3, and the root of the zygoma is more directly opposite M^1.

The zygomatic arch of *Gymnurechinus* is nearly horizontal, as in *Neurogymnurus* and *Amphechinus*, whereas in Recent Erinaceinae it rises towards the posterior end. The ventral process which occurs near the anterior end of the zygoma in Recent Erinaceinae, for the origin of the most anterior fibres of the masseter muscle, is lacking in *Gymnurechinus*, as in *Amphechinus* and *Neurogymnurus*. As in other Erinaceidae, the zygomatic process of the maxilla of *Gymnurechinus* meets that of the squamosal, and the jugal is a small bone on the lateral side of the zygoma.

CRANIAL ROOF.—The frontals closely resemble those of *Amphechinus* and *Neurogymnurus*. They are not extensively overlapped by the parietals, but the fronto-parietal suture is approximately transverse. The frontals are not swollen out by the dorsal part of the olfactory chamber, and the postorbital processes are rather more distinct than in *Amphechinus* and *Neurogymnurus*. There is a marked postorbital constriction of the cranium, as in *Amphechinus* and other primitive Erinaceidae. Strong frontal crests arise from the postorbital processes and converge to form the sagittal crest near the fronto-parietal suture. Over the parietals the sagittal crest is broad, flat-topped and rectangular in cross-section. In *Amphechinus* it is sharper and more elevated. In *Neurogymnurus* it is usually paired, but the holotype of *Cayluxotherium elegans* has a median, rather low crest. On the interparietal, the sagittal crest of *Gymnurechinus* consists of a median crest with weak subsidiary crests on its sides; these lateral crests unite anteriorly to form the main sagittal crest over the parietal, but the median crest is confined to the interparietal. Except that the lateral crests are better developed and more distinct from the median crest, a very similar structure occurs in the skull of *Neurogymnurus* in the British Museum, regd. no. M3752. (Pl. 3, figs. 20 & 27.)

A number of venous foramina occur near and above the parietal-squamosal suture (postparietal foramina). Viret (1938, fig. 1) figures foramina in *Amphechinus* in a

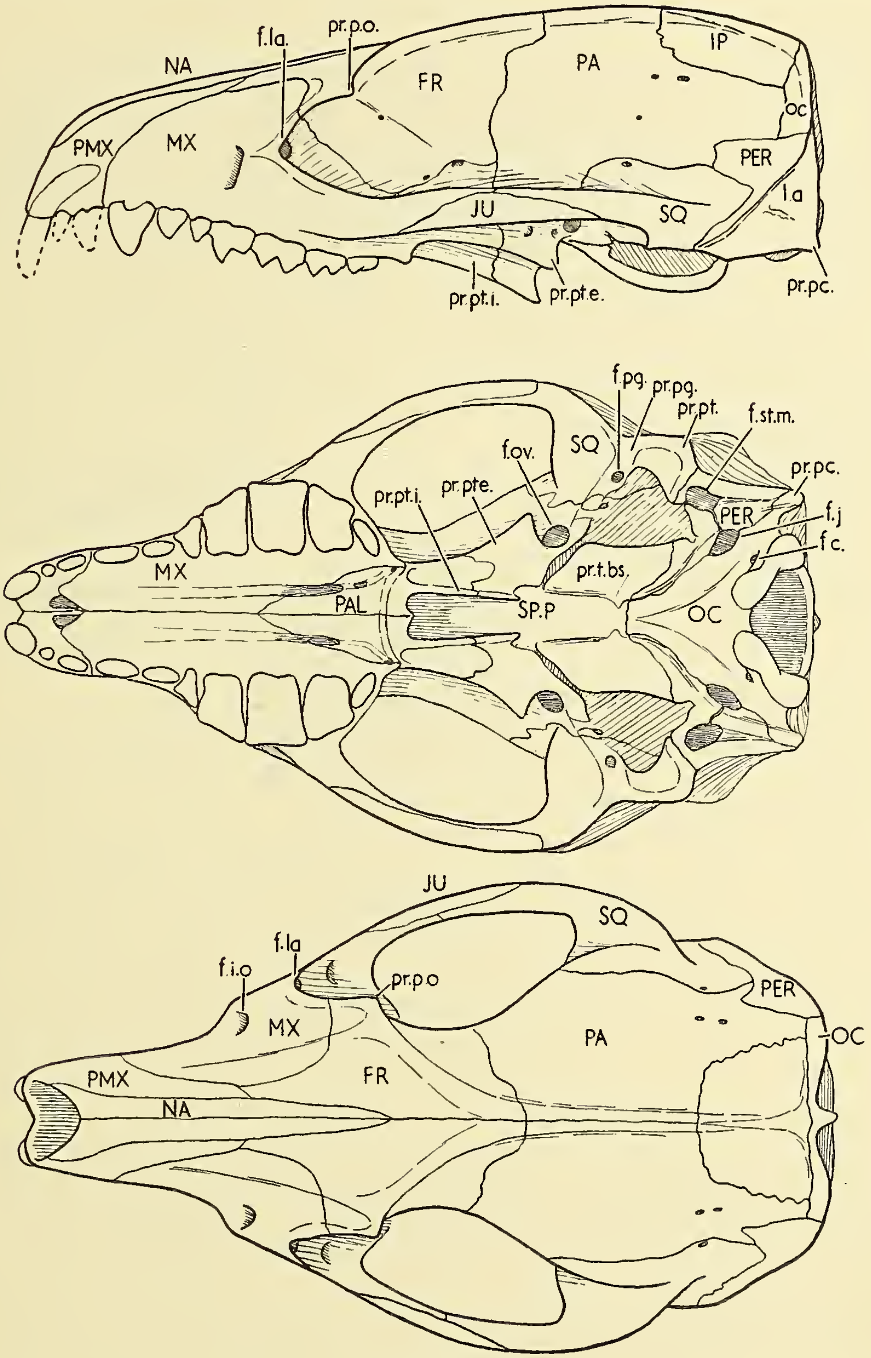

Fig. 1. Skull of *Gymnurechinus leakeyi*. Restoration based mainly on the holotype and Rs 491.51. ×2. *FR*, frontal; *IP*, interparietal; *JU*, jugal; *MX*, maxilla (to which the lachrymal is fused); *NA*, nasal; *OC*, occipital; *PA*, parietal; *PAL*, palatine; *PER*, periotic; *PMX*, premaxilla; *SP.A*, anterior sphenoid (orbitosphenoid+presphenoid+ethmoid); *SP.P*, posterior sphenoid (basisphenoid+alisphenoid).

f.c., condylar foramen; *f.i.o*, infraorbital foramen; *f.j*, jugular foramen; *f.la*, lachrymal foramen; *f.ov*, foramen ovale; *f.pg*, postglenoid foramen; *f.st.m*, stylomastoid foramen; *l.a*, lambdoid area; *pr.pc*, paroccipital process; *pr.pg*, postglenoid process; *pr.p.o*, postorbital process; *pr.p.t*, post-tympanic process; *pr.pt.e*, external pterygoid process; *pr.pt.i*, internal pterygoid process; *pr.t.bs*, tympanic process of basisphenoid.

similar position; in Recent Erinaceinae only the foramen near the upper edge of the squamosal persists.

The interparietal is semicircular; in *Neurogymnurus* it is triangular; in *Amphechinus*, and especially in Recent Erinaceinae its exposed portion is more transverse, owing to more or less extensive overlap by the parietal. The sagittal crest ends posteriorly in a small elevated quadrangular area, across which passes the suture between the interparietal and occipital. This suture passes in front of the occipital (nuchal) crest, which is therefore formed from the occipital bone. The occipital crest is very high, much as in *Echinosorex*, as may be seen best in Rs 1.49. At its lower end it divides into the two lambdoid crests, which are formed from the periotic (mastoid exposure). The anterior lambdoid crest passes obliquely forward to the post-tympanic process, while the posterior lambdoid crest runs vertically to the paroccipital (paracondyloid) process. The posterior lambdoid crest is much more strongly developed than in *Amphechinus* and Recent Erinaceinae, and resembles that of *Neurogymnurus*, in which, however, the anterior lambdoid crest is peculiarly modified (Butler 1948). The two lambdoid crests enclose a triangular area, which might be termed the lambdoid area, deeply pitted for insertion of the splenius and trachelomastoid muscles. Unlike Recent Erinaceidae, the mastoid exposure extends up the side of the skull above the anterior lambdoid crest. A similar mastoid extension occurs in the British Museum specimen of *Neurogymnurus*, and a rather smaller extension is present in the holotype of *Amphechinus edwardsi*.

The zygomatic process of the squamosal is deeply concave laterally. Its upper edge is continued backwards as a crest which ends above the post-tympanic process, and does not meet the anterior lambdoid crest.

The surface of the parietal, interparietal and squamosal is marked by a complex system of ridges, which seem to be related to the origin of the temporalis muscle (Plate 3, fig. 20). The ridges are most strongly developed near the occipital crest, weaker and somewhat more regular over the lateral part of the parietal and the upper part of the squamosal; they are lacking from an area on the dorsal part of the parietal, near the sagittal crest. In the anterior part of the area affected, the general course of the ridges is from anterodorsal to posteroventral; near the occipital crest they are less regular, but tend to lie parallel to the crest. The ridges unite at intervals to enclose small lenticular areas or shelves. Each ridge is obliquely placed in relation to the surface of the bone, the anterior or anteroventral face being steeper than the posterior or posterodorsal face. The ridges are obviously comparable with those of *Neurogymnurus*, in which there is a rather similar arrangement (Plate 3, fig. 27), but in *Gymnurechinus* they do not give the impression of having been formed by the fusion of separate nodules. Similar, but somewhat weaker, ridges occur in *Amphechinus*; in old specimens of *Erinaceus* the surface of the parietal is marked very faintly with irregularities which have a similar direction to those of *Gymnurechinus* (Plate 3, fig. 23), and in some specimens of *Echinosorex* a system of very faint ridges extends widely over the temporal area.

PALATE.—The palate is incompletely visible in the holotype, but is well exposed in Rs 491.51 (Plate 2, fig. 13), Rs 1.49 and Rs 623.50. As in other Erinaceidae, the premaxilla forms only a small part of the palate, the maxilla extending forward to the level of I^2 (Rs 491.51). The palatine bone extends nearly as far forward in the palate

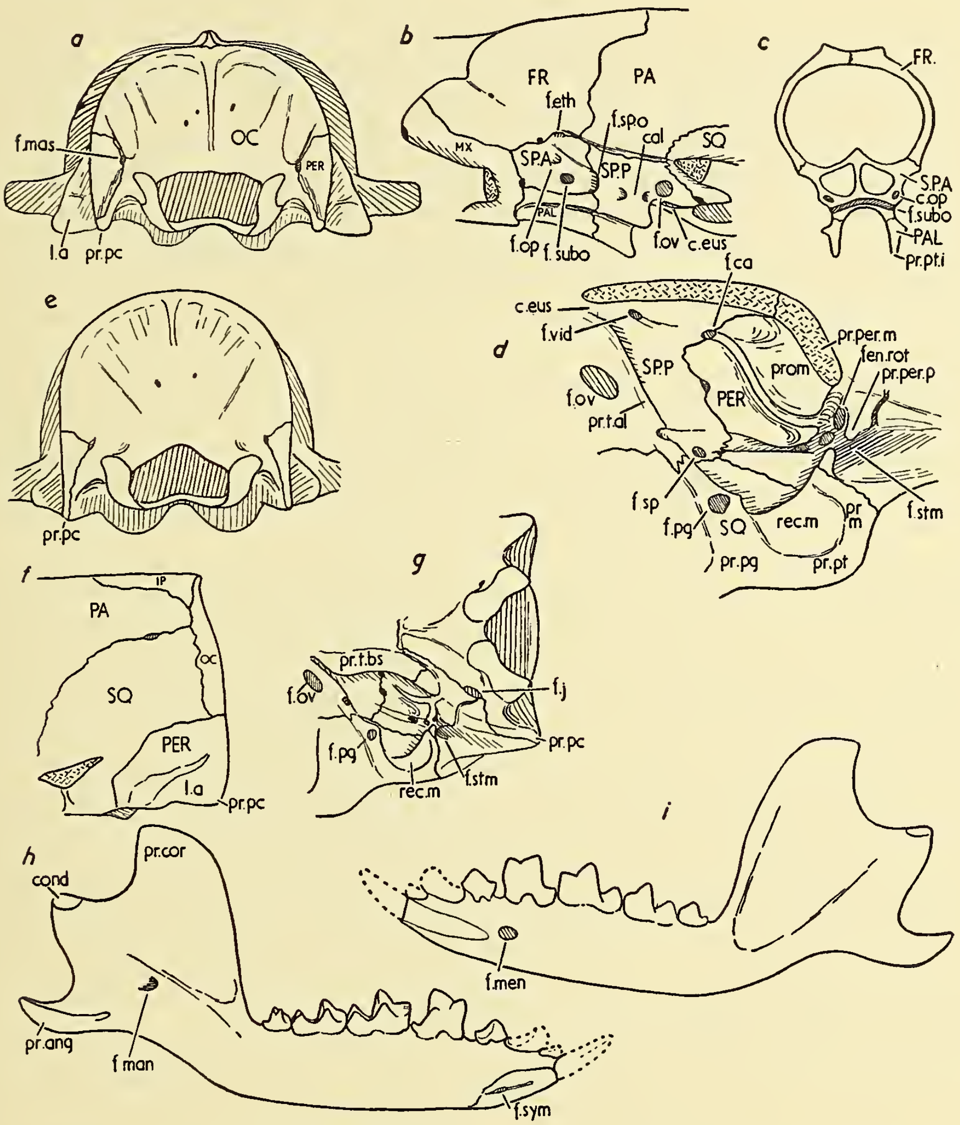

Fig. 2. *Gymnurechinus leakeyi*. (*a*) Posterior view of skull. (*b*) Orbitotemporal region in left side view. The zygomatic arch is represented as removed. (*c*) Transverse section through the skull at the level of the suboptic foramen. Below the anterior end of the brain-cavity is seen the posterior extremity of the olfactory chamber. Rs 1.49, slightly restored. (*d*) Roof of right tympanic chamber and adjacent structures. Based on Rs 402.50.

Neurogymnurus cayluxi, B.M. M3752. (*e*) Posterior view of skull. (*f*) Side view of posterior part of skull to show sutures. (*g*) Ventral view of tympanic and basioccipital regions.

Gymnurechinus leakeyi. (*h*), (*i*) Medial and lateral views of lower jaw.

All drawings are restorations, ×2, except (*d*) which is ×4.

c.al, alisphenoid canal; *c.eus*, eustachian canal; *c.op*, canal for optic nerve; *f.ca*, carotid foramen; *fen.rot*, fenestra rotunda; *f.eth*, ethmoid foramen; *f.j*, jugular foramen; *f.man*, mandibular foramen; *f.mas*, mastoid foramen; *f.men*, mental foramen; *f.op*, optic foramen; *f.ov*, foramen ovale; *f.pg*, postglenoid foramen; *f.sp*, foramen spinosum; *f.sp.o*, sphenorbital foramen; *f.st.m*, stylomastoid foramen; *f.subo*, suboptic foramen; *f.sym*, symphysial foramen; *f. vid*, posterior opening of vidian canal; *l.a*, lambdoid area; *pr.ang*, angular process; *pr.cor*, coronoid process; *pr.m*, mastoid process; *prom*, promontorium; *pr.pc*, paroccipital process; *pr.per.m*, median tympanic process of the periotic; *pr.per.p*, posterior tympanic process of the periotic; *pr.pg*, postglenoid process; *pr.p.t*, post-tympanic process; *pr.pt.i*, internal pterygoid process; *pr.t.al*, tympanic process of the alisphenoid; *rec.m*, recessus meatus. Other lettering as in Fig. 1.

as the anterior end of M^1, as in *Neurogymnurus*; in *Amphechinus edwardsi* it reaches slightly beyond M^1, but in the Recent Erinaceidae it is a little shorter, ending usually opposite the middle of M^1. A groove for the palatine artery and nerve may be seen on the maxilla parallel to the median suture, and leading back to a foramen just behind the palatine-maxillary suture. This foramen is enlarged, especially on Rs 491.51, to form a rudimentary slit-like fenestra. Behind this in Rs 491.51 there is a smaller opening, represented in Rs 623.50 by two small foramina. Somewhat similar slit-like palatal vacuities occur in *Dimylechinus bernoullii* (Hürzeler 1944, fig. 3) and some specimens of *Amphechinus edwardsi* (Viret 1929, pl. **1**, fig. 1). The palatal perforation of *Neurogymnurus* (seen in the holotype of *Cayluxotherium elegans*) is an artefact.

There is a well-developed transverse crest across the palate behind M^3, pierced on each side by a foramen (Rs 491.51). The hard palate ends almost immediately behind the transverse crest, as in *Amphechinus* and *Neurogymnurus*. The external pterygoid processes are narrower anteriorly than in Recent Erinaceinae, and are formed to a greater extent from the alisphenoid and less from the palatine; they show most resemblance to those of *Hylomys* among the Recent forms.

ORBITOTEMPORAL REGION (Text-fig. 2*b*). As in other Erinaceidae, the maxilla and frontal contribute extensively to the inner wall of the orbit. The maxilla does not, however, approach the alisphenoid, as in Recent Erinaceinae, but the orbitosphenoid remains exposed in lateral view as much as in *Hylomys*, *Neurogymnurus* and *Amphechinus* (Butler 1948). Below the optic foramen, which as in other Erinaceidae is comparatively small, is a larger suboptic foramen, leading to a transverse venous canal through the anterior sphenoid. The suboptic foramen of *Gymnurechinus* is fully exposed in lateral view, as in other primitive Erinaceidae, whereas in Recent Erinaceinae it is hidden by the flange of the alisphenoid that forms the lateral border of the sphenorbital foramen. From the top of the latter foramen an oblique flange passes anterodorsally across the orbitosphenoid, above the optic foramen, as in *Neurogymnurus* and *Amphechinus*. There is no separate foramen rotundum. An alisphenoid canal is normally present, but it is absent in Rs 402.50.

As in other Erinaceidae, there is a well-developed ethmoid foramen near the suture between the frontal and the orbitosphenoid, for the lateral cerebral vein. Shortly anterior to this, just above the suture, is a small foramen for a vessel which passes up the side of the olfactory lobe of the brain. Another small foramen, opening forwards, occurs near the upper edge of the orbit, behind the postorbital process. These two small foramina occur in similar positions in *Amphechinus* (Hürzeler 1944, fig. 2), and the foramen near the postorbital process can be seen in the cranium of *Neurogymnurus* regd. M3752 in the British Museum. In *Erinaceus* and *Echinosorex* the two foramina are situated much nearer to the ethmoid foramen.

The lower edge of the origin of the temporal muscle is marked by a low crest which passes forward from the posterior root of the zygoma, near the suture between the alisphenoid and the parietal. It is present, though weaker, in *Erinaceus*.

BASICRANIAL REGION (Text-figs. 1, 2*d*, 2*g*, 9*a*).—This part of the skull shows a close resemblance to *Neurogymnurus*.

The internal pterygoid process continues back as a small flange which forms the lateral border of the eustachian canal and, in *Erinaceus*, provides attachment for part of the tensor palati muscle. In *Erinaceus* the more lateral fibres of this muscle are attached to the anterior border of the tympanic bone.

The medial wall of the large tympanic chamber, formed mainly by the tympanic process of the basisphenoid, is continued backwards by a medial tympanic process of the periotic. There is no basisphenoidal pit, but the posterior border of the pit is represented by a flange passing down the medial side of the tympanic process, just anterior to the basioccipital-basisphenoid suture.

The anterior wall of the tympanic chamber is formed by a flange of the alisphenoid which is continuous with the external pterygoid process on the medial side of the foramen ovale. Near the foramen ovale this flange would give rise to the sphenomandibular ligament. A notch in its edge marks the exit of the infraorbital branch of the stapedial artery from the tympanic chamber. The tympanic process of the alisphenoid is continued across the squamosal by a similar flange terminating laterally in the postglenoid process. The postglenoid foramen opens behind the edge of this flange, as in *Amphechinus*, and does not interrupt it as in *Erinaceus*.

The postglenoid process is joined to the post-tympanic process by a crest which forms the upper border of the external auditory meatus. Internal to this is a shelf of bone which forms the upper surface of the recessus meatus, better developed than in *Erinaceus*. This shelf is formed entirely from the squamosal, as in *Neurogymnurus* and *Echinosorex*, whereas in *Erinaceus* it is formed partly from the periotic. Similarly the post-tympanic process of *Gymnurechinus* and other primitive Erinaceidae, formed from the squamosal, is replaced in *Erinaceus* by a mastoid process, formed from the periotic. The true mastoid process of *Gymnurechinus* is represented by the posterior border of the recessus meatus, medial to the post-tympanic process. Further medially again is the styloid process, which forms the lateral border of the stylomastoid foramen. The medial border of the foramen is formed by the posterior tympanic process of the periotic, which roofs over the fenestra rotunda from behind. The common carotid artery enters the tympanic chamber between the posterior and medial tympanic processes of the periotic.

The paroccipital processes are more strongly developed than in Recent Erinaceinae, and are separated from the condyles by deeper notches. Each paroccipital process is connected to the mastoid process by a longitudinal crest which forms the lower edge of the lambdoid area; in *Amphechinus* and Recent Erinaceinae this is notched or interrupted by the hyomandibular nerve. A more medial crest runs from the paroccipital process to the medial side of the stylomastoid foramen; in *Amphechinus* and Recent Erinaceinae this is notched or broken by the jugular foramen, but in *Gymnurechinus* it is complete, the jugular foramen being placed well to the medial side of the crest. A groove passes from the jugular foramen down the medial side of the crest, probably for the auricular branch of the vagus nerve; it is present also in *Neurogymnurus*, but is only faintly indicated in *Echinosorex* and *Erinaceus*. In this part of the skull, *Amphechinus* resembles *Erinaceus*, whereas *Gymnurechinus* resembles *Neurogymnurus*.

TYMPANIC CHAMBER (Text-fig. 2*d*; Pl. 3, fig. 22).—The roof of the tympanic chamber (best seen in Rs 402.50) is again very similar to that of *Neurogymnurus* (Text-fig. 2*g*, and Butler 1948, fig. 9). It is formed from the sphenoid as well as the periotic, the sphenoid contribution being much more extensive than in *Erinaceus*. The carotid artery, after entering the chamber between the two tympanic processes of the periotic, divides into the stapedial and internal carotid arteries, the courses of which can be followed as grooves on the promontorium. The internal carotid runs anteromedially to enter the skull by the carotid foramen in the suture between the sphenoid and periotic. Further forward, near the eustachian canal, is the opening of the vidian canal. The stapedial artery enters the facial groove, which in *Gymnurechinus* is almost roofed over by flanges of bone, concealing the facial foramen. A foramen spinosum for the middle meningeal artery (ramus superior arteriae stapediae) occurs in the alisphenoid near the suture with the squamosal. The concavity for the tensor tympani muscle is deep.

Three fragments of bone were found in the tympanic chamber of the holotype. One of these appears to be part of the tympanic bone. It is flattened, roughly rectangular, and placed next to the tympanic process of the basisphenoid, in the anterior part of the chamber. If correctly identified, it would indicate that the tympanic was a comparatively broad bone like that of the Recent Erinaceinae or *Neurogymnurus*. It must have been loosely attached, as there is no trace of it in the other skulls.

A second fragment, which was found in the anterolateral part of the chamber, near the postglenoid foramen, and which has been removed intact, may with some hesitation be identified as the head of the malleus (Text-fig. 3). There is a well-marked anterior groove which resembles that on the processus gracilis mallei of *Erinaceus*, where it articulates with the tympanic bone; opening into this groove is the foramen for the chorda tympani. The surface which articulates with the incus is not well preserved, but it does not seem to approach the anterior end as closely as in *Erinaceus*, being preceded by an anterior convexity. The neck of the malleus is much thicker than in *Erinaceus*, and the lamina is correspondingly stout. The fragment indicates that the malleus was similar in size to that of *Erinaceus europaeus*.

The third fragment appears to belong to the hyoid apparatus, and is described below.

OCCIPITAL REGION (Text-figs. 2*a* & 9*d*; Pl. 3, fig. 21).—The foramen magnum faces more ventrally than in Recent Erinaceinae, resembling that of *Neurogymnurus*, *Amphechinus* and *Echinosorex*. It does not rise above the top of the condyles, and shows no sign of the embayment of the upper border which usually occurs in Recent Erinaceinae. The condyles project below the ventral surface of the skull. The anterolateral border of the condyle is notched near the condylar foramen, so that in ventral view the condyle appears dumb-bell shaped. In posterior view the condyle extends dorsally and laterally, and its lateral border is marked by another notch. In Recent Erinaceinae the condyles are simpler, and do not extend so far dorsally.

Seen in posterior view, the occipital crest, with the posterior lambdoid crests, forms a semi-ellipse, resembling *Neurogymnurus*, but broader in relation to its height. In *Amphechinus* the crest rises to a point dorsally, so that the occipital surface is more triangular (Viret 1938, fig. 2); in *Erinaceus* the dorsal part of the crest is nearly horizontal, giving the skull a trapezoidal shape in occipital view.

From the posterior end of the sagittal crest, a sharp median crest passes down the occipital surface of the skull, to end just above the upper edge of the foramen magnum. Laterally to this crest is a concavity for the insertion of the m. rectus capitis posticus minor. The median crest is equally well developed in *Amphechinus*, but it is much weaker in *Neurogymnurus*, *Echinosorex* and the Recent Erinaceinae. The posterior face of the skull above the foramen magnum is much roughened for muscle attachment and is pierced by a number of small foramina.

The lateroventral part of the occipital surface, medially to the posterior lambdoid crest, is occupied by a deep pit for the insertion of the m. obliquus capitis superior. The lateral part of this pit is formed from the mastoid exposure, and the mastoid foramen opens at the bottom of the pit. In Recent Erinaceinae the mastoid foramen usually closes in the adult.

LOWER JAW.—The lower jaw (Text-fig. *2h*, *2i*; Pl. **1**, fig. 3) resembles that of *Amphechinus* in the low position of the condyle and the backwardly sloping anterior border of the coronoid process. The angle of elevation of the condyle, measured from the base of the coronoid process (Butler 1949, fig. 20), is 28°, as compared with 20–26° in *Amphechinus*[*] and 36–43° in Recent Erinaceinae. The elevation of the anterior edge of the coronoid process is 74°, as compared with 70–80° in *Amphechinus*[*] and about 90° in Recent Erinaceinae. The tip of the angular process is slightly below the alveolar level of the molars, as in *Amphechinus*, whereas in Recent Erinaceinae it is above this level.

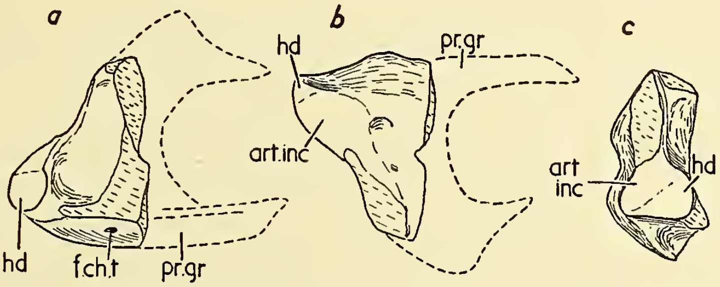

FIG. 3. *Gymnurechinus leakeyi.* Malleus from Rs 12.32. ×10. (*a*) inner, (*b*) outer, (*c*) posterior views.
art.inc, articular surface for incus; *f.ch.t*, foramen for chorda tympani; *hd*, head of malleus; *pr.gr*, processus gracilis.

The coronoid process resembles that of *Amphechinus* in its relatively broad tip. The mandibular foramen is situated as in *Amphechinus* and *Neurogymnurus* about half-way between the condyle and the base of the coronoid process, whereas in Recent Erinaceinae, except *Atelerix albiventris*, it is nearer to the base of the coronoid process. The oblique crest above the foramen, for attachment of the posterior part of the mylohyoid muscle and the sphenomandibular ligament, is more strongly developed than in Recent Erinaceinae. The condyle is not widened transversely as in Recent Erinaceinae: the width is 38% of the alveolar molar length, as compared with 27–37% in *Amphechinus cayluxi*, 39–44% in *A. edwardsi*, and 40–47% in Recent Erinaceinae. Just below the condyle is a convexity on the posterior edge of the condylar process, probably for attachment of part of the capsular ligament of the jaw joint; it is equally well developed in some specimens of *Amphechinus*, weaker in others, and hardly indicated in Recent Erinaceinae.

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[*] These measurements refer to *A. edwardsi* and related species. In *A. intermedius* the posterior end of the jaw is more elevated.

The angular process, as in other Erinaceidae, possesses a flange on the medial side for the insertion of the internal pterygoid muscle. The lower edge of the angular process is sharp, and the outer face does not show the convexity found in many Recent Erinaceinae, but is very slightly concave.

The horizontal ramus varies in depth, probably with age. It is relatively longer than in Recent Erinaceinae, in accordance with the greater length of the snout. The mental foramen is below the anterior root of P_4, as in most specimens of *Amphechinus*. The tip of the jaw is preserved in the holotype, in Rs 1971.50, and in Rs 588.50. These specimens show that the symphysis extends back to near the posterior end of P_2, and that a foramen opens on the symphysial surface, near its posterior end, as in other primitive Erinaceidae. (For measurements see Table 3.)

HYOID.—Three pieces of bone associated with the type specimen are believed to represent part of the hyoid apparatus. Lying longitudinally in the left tympanic chamber, above the supposed tympanic, is a slender rod, 4·2 mm. in length and slightly flattened in cross-section. It is broken anteriorly, where its greatest diameter is about 0·7 mm. It is too long to be the manubrium mallei, and may tentatively be identified as the stylohyal.

Two rod-like pieces of bone lie against the basisphenoid, wedged between the tympanic processes. The shorter of the two pieces, which is 4·6 mm. long and 1·9 mm. in greatest breadth, appears to be complete, and shows a facet for a joint at its posterior end. This could be the ceratohyal, which is relatively short in Erinaceinae. It is flattened and somewhat twisted. The other bone, which lies along the right side of the first, is somewhat longer and possibly incomplete. As preserved, its length is 5·1 mm. and its greatest width 1·5 mm. This might be the thyreohyal.

THE BRAIN-CAST.—The greater part of the brain-cast is visible in Rs 1.49 and Rs 12a.32 (Pl. **1**, figs. 4–8). Rs 32.32 also shows part of the ventral surface. The three specimens permit the reconstruction of almost the whole of the brain-cast (Text-fig. 4).

The only fossil erinaceid brain-cast hitherto known is that of *Galerix exilis* (described as *Parasorex socialis*, Edinger 1928), of which the ventral aspect is unknown. A plaster cast of the endocranial surface of the skull roof of *Neurogymnurus* sp. (M9653a) has been prepared at the British Museum (Pl. 4, fig. 32), and rubber latex casts have been made of the cranial cavities of *Echinosorex gymnurus* and *Erinaceus europaeus*. The brain-cast of *Erinaceus* has been figured by Gervais (1872) and by Olson (1944). The brain of *Erinaceus* has been studied by dissection. Reference has also been made to the description of the brains of *Echinosorex* and *Erinaceus* by Le Gros Clark (1932).

Comparative measurements are given in Table 8. Measurements made on the rubber casts have been checked against direct measurements of the skulls. The specimen of *Neurogymnurus* from which the endocranial cast has been prepared is about 1·3 times the size of M3752 (Butler 1948). The skull is distorted by crushing, and the cast has been reconstructed by comparison with the skull registered M3752, allowance being made for the greater size.

The brain-cast of *Gymnurechinus leakeyi* agrees fairly closely in length with those of *Erinaceus* and *Neurogymnurus*, but it is narrower. The product, total length × maximum breadth × height of cerebrum, is 5·6 cu. cms. in *Gymnurechinus*, 6·9 cu. cms. in *Erinaceus* and 12 cu. cms. in *Echinosorex*. The ratio, total length/maximum breadth, is greater in *Gymnurechinus* (1·58) and *Echinosorex* (1·62) than in *Erinaceus* (1·29) and *Galerix* (1·33). In *Neurogymnurus* the cast of the anterior end of the olfactory bulbs is not visible; if the olfactory bulbs are excluded, the ratio length/breadth is the same in *Neurogymnurus* as in *Galerix* and *Erinaceus* (1·02), and less than in *Echinosorex* and *Gymnurechinus* (1·28). The ventral length of the brain is also relatively greater in *Gymnurechinus* and *Echinosorex* than in *Erinaceus* (Table 9).

The proportions of the endocranial cavity can be determined approximately from measurements made on the outer surface of the skull, since in the Erinaceidae no air-spaces exist within the bones that cover the brain. Thus the greatest width across the cerebrum is a little less than the width of the cranium measured across the squamosals above the glenoid surfaces, the anterior end of the ventral surface of the brain is above the suboptic foramen, and the posterior end of the cerebellum is at the inner dorsal border of the foramen magnum. In this way it may be shown that *Hemiechinus auritus*, *Amphechinus edwardsi* and *Brachyerix* agree with *Erinaceus* and *Neurogymnurus* in possessing relatively short brains, while *Hylomys* and *Neotetracus* have longer brains like *Echinosorex* and *Gymnurechinus*. The same result is obtained if the measurement of length is made from the narrowest part of the skull between the orbits, representing the position of the anterior end of the cerebral hemispheres (Table 10).

The long-brained Erinaceidae differ from the short-brained forms in the greater length as compared with the width, of the cerebral hemispheres, the cerebellum, and the base of the brain anterior to the foramina ovalia. They also differ in the longer dorsal exposure of the cerebellum, in proportion to the length of the cerebral hemispheres. These differences appear to be due to a lesser degree of longitudinal compression of the brain in *Gymnurechinus* and the Echinosoricini.

DETAILS OF THE CAST.—The surface of the olfactory bulbs which is in contact with the cribriform plate is not visible on the casts. The anterior end of the brain-cavity has, however, been cleared of matrix in Rs 491.51 and Rs 623.50; and the olfactory bulbs are shown to be longer than is apparent in Rs 1.49. The olfactory tubercle is partly exposed in all three specimens of the brain-cast. It is about 5 mm. in length, and extends laterally about 3 mm. from the optic nerve. Its surface is slightly convex, with very faint irregularities, and is marked by a shallow transverse furrow, just anterior to the root of the optic nerve. It is very much like the olfactory tubercle in the endocranial cast of *Echinosorex*.

The rhinal fissure is covered for part of its length by the lateral cerebral vein, but it may be seen anteriorly and posteriorly. At its posterior end it turns dorsomedially as in *Echinosorex*. The pyriform lobe is similar in proportions to that of *Echinosorex*; it is 15 mm. in length and 6·8 mm. in height, seen in side view. It is exposed in ventral view in Rs 32.32. Lateral to the root of the mandibular nerve are two swellings, a smaller more medial one which probably represents the gyrus lunaris, and a more prominent lateral one which seems to correspond with the gyrus ambiens. Similar swellings occur in *Echinosorex*, in which, however, the gyrus lunaris is less prominent.

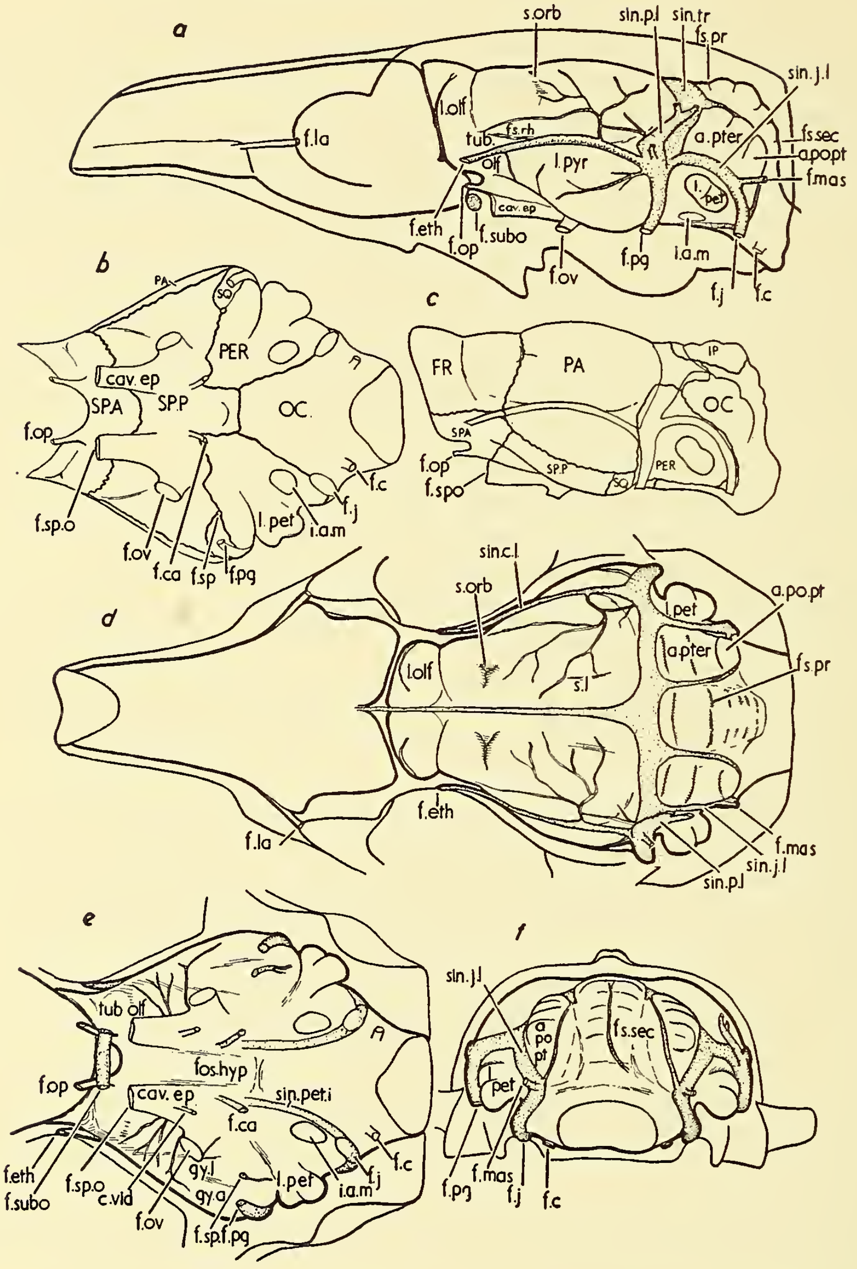


Fig. 4. *Gymnurechinus leakeyi*. Restoration of endocranial cast, from Rs 1.49, Rs 12a.32 and Rs 32.32. × 2.

(*a*), (*d*), (*e*) and (*f*) show respectively lateral, dorsal, ventral and posterior views of the brain-cast; on (*a*) and (*d*) the outline of the olfactory chamber is indicated. (*b*) and (*c*) show the positions of sutures in the interior of the brain-cavity.

a.po.pt, area postpterotica; *a.pter*, area pterotica; *cav.ep*, cavum epiptericum; *c.vid*, vidian canal; *fos.hyp*, fossa hypophyseos; *fs.pr*, fissura prima; *fs.rh*, fissura rhinalis; *fs.sec*, fissura secundaria; *gy.a*, gyrus ambiens; *gy.l*, gyrus lunaris; *i.a.m*, internal auditory meatus; *l.olf*, olfactory lobe; *l.pet*, petrosal lobule of the paraflocculus; *l.pyr*, pyriform lobe; *sin.c.l*, lateral cerebral venous sinus; *sin.j.l*, lateral jugular vein; *sin.pet.i*, inferior petrosal sinus; *sin.p.l*, posterolateral sinus; *sin.tr*, sinus transversus; *s.l*, longitudinal sulcus; *s.orb*, sulcus orbitalis; *tub.olf*, olfactory tubercle. Other lettering as in Figs. 1 and 2.

The neopallium is 13 mm. long and 8 mm. broad at its greatest width in dorsal view. In *Erinaceus* the corresponding measurements are 13 × 8·6 mm., in *Echinosorex* 17 × 9·6 mm., and in *Neurogymnurus* 15 × 9 mm. About 3 mm. from the anterior end there is a well-marked sulcus orbitalis, which closely resembles those of *Galerix* and *Echinosorex*; it is weaker in *Erinaceus*. Near the posterior end, about 2·5 mm. from the medial border, is a longitudinal sulcus, about 5 mm. in length, which occurs in the brain-cast of *Echinosorex* but not in *Erinaceus*. It cannot be distinguished in *Neurogymnurus*, in which, however, another longitudinal sulcus occurs further forward and more laterally.

The canal for the optic nerve has about the same diameter as in *Erinaceus*. It is about 3 mm. long, as against 4 mm. in *Erinaceus*. It passes directly forward through the anterior sphenoid, as in *Erinaceus* and *Echinosorex*. The base of the brain-cast, in the region of the optic chiasma and sella turcica, is for the most part not exposed, but it is possible to see that the dorsum sellae is weak, as in Recent Erinaceidae. The base of the brain-cast, between the foramen ovale and the internal opening of the optic foramen, was longer and narrower in *Gymnurechinus* than in *Erinaceus*; the proportions resemble those of *Echinosorex*.

The roof of the mid-brain is not exposed, the short interval between cerebrum and cerebellum being filled, as in Recent Erinaceidae, with the sinus transversus. Edinger (1928) is probably incorrect in interpreting the region between the cerebrum and cerebellum of *Galerix* as an exposure of the corpus quadrigeminum posterior.

The foramen ovale (mandibular branch of nerve V) is similar to that of *Echinosorex* in facing more rostrally than in *Erinaceus*. The other branches of V, together with the nerves to the eye-muscles, pass forward in a canal under the base of the brain (cavum epiptericum), which opens as the sphenorbital foramen. The vidian canal (palatine branch of VII) opens into the floor of the cavum epiptericum internally to the foramen ovale, as in *Erinaceus* and *Echinosorex*. In the basioccipital region the brain-cast shows a slight swelling for the pons, and the internal auditory meatus (VII, VIII), the jugular foramen (IX, X, XI) and the single condylar foramen (XII) can be made out.

The cerebellum is best exposed in Rs 12a.32; the dorsal part is visible in Rs 1.49. In all erinaceid brain-casts the cerebellum shows a tripartite structure, the hemispheres being separated from the vermis by paramedian grooves which are, however, much shallower in *Erinaceus* than in the more primitive forms. In *Erinaceus*, *Neurogymnurus* and *Galerix* the cerebellum seems to have made less impression on the endocranial surface than in *Gymnurechinus* and *Echinosorex*; in *Gymnurechinus* the impression is particularly detailed.

A deep transverse sulcus, visible also in *Echinosorex*, crosses the vermis just anterior to its highest point. Further forward there is another transverse sulcus, in front of which the cerebellum is overlain by the sinus transversus; this anterior sulcus may be the fissura prima. On the posterior surface of the vermis there are five transverse sulci, of which the fifth is the deepest, and may be the fissura secundaria. Below this there seems to be a very faint sixth sulcus. Four main folia can be distinguished in each cerebellar hemisphere, of which the third, which is the most prominent posterodorsally, shows faint signs of subdivision; the two anterior folia apparently represent the area pteroidea, the two posterior the area post-pteroidea.

In front of the first folium there is visible in Rs 1.49 part of a more anterior area, which may represent another folium, so that the area pteroidea would be tripartite as in *Echinosorex*. The main part of the paraflocculus is hidden by the lateral jugular vein, but the petrosal lobule is well developed. It is larger than in the Recent forms: it is 3·2 mm. long and 3·3 mm. high; the fossa in the periotic bone is over 3 mm. deep. In *Echinosorex* the parafloccular fossa measures 3·2 × 2·6 mm., and is about 2·5 mm. deep; in *Neurogymnurus* it is about the same size as in *Echinosorex*; in *Erinaceus* it is only 1·7 mm. in diameter, and its depth varies from 1·2 mm. to practically nothing.

INNER WALL OF THE BRAIN-CAVITY.—The brain-casts show indications of the position of the sutures between the bones which appear on the endocranial surface (Text-figs. 4*b*, 4*c*). Differences from *Erinaceus* and *Echinosorex* are slight.

The frontal extends back to the sulcus orbitalis, where it meets the parietal: in Rs 1.49 the suture on the left side is a little further back than on the right. The olfactory lobes end dorsally about 1·5 mm. behind the postorbital processes. The frontal extends down the side of the anterior part of the brain to the level of the lateral cerebral vein, where it meets the orbitosphenoid. The latter bone cannot be distinguished from the presphenoid and ethmoid: the combined bone may be called the anterior sphenoid. Together with the frontals, it encloses the anterior end of the brain, and meets the parietal posterolaterally and the posterior sphenoid posteriorly.

The parietal forms a large part of the cranial roof, extending down at the sides as far as the most lateral part of the pyriform lobe. Its suture with the interparietal lies above the sinus transversus. More laterally it meets the occipital over the anterior part of the cerebellar hemisphere. The suture between the interparietal and the occipital passes in front of the highest point of the vermis; this suture closes in adult *Erinaceus*, but not in *Gymnurechinus* or *Echinosorex*; Edinger (1928) noted its presence in *Galerix*, and it occurs also in *Neurogymnurus*.

The squamosal is almost excluded from the endocranial wall by the alisphenoid, periotic and parietal, but it reaches the brain over a small area at the posterolateral end of the pyriform lobe. This is true also of *Erinaceus*, *Echinosorex* and, probably, *Neurogymnurus*.

The alisphenoids and basisphenoid are united to form one bone (posterior sphenoid) which meets the anterior sphenoid behind the middle of the olfactory tubercle and covers the lower surface of the pyriform lobe. Posteriorly it meets the occipital, periotic and squamosal. The periotic touches the posterior end of the pyriform lobe, and sends an extensive flange beneath the parietal: its dorsal suture passes laterally to the cerebellar hemisphere. The occipital, a single bone as in other adult Erinaceidae, covers the greater part of the vermis and hemispheres of the cerebellum; ventrally it passes forward between the periotics to meet the posterior sphenoid just behind the clinoid process.

BLOOD-VESSELS VISIBLE ON THE BRAIN-CAST.—The most important venous exit from the skull is the postglenoid foramen. This leads to a space bounded by the squamosal and parietal externally and the periotic internally. The lateral cerebral vein, which enters the skull by the ethmoid foramen near the lower edge of the frontal, opens into this space anteriorly after passing back in a groove on the internal face of the parietal. In *Erinaceus*, *Echinosorex* and *Neurogymnurus* the lateral cerebral vein follows a nearly straight course across the pyriform lobe, below the rhinal fissure, and converges towards the fissure posteriorly; in *Gymnurechinus*, however, the vein rises in an arc, and for most of its course follows the rhinal fissure.

A number of other vascular channels also converge towards the postglenoid foramen. Below the lateral cerebral vein some small vessels are received from the posterior end of the pyriform lobe. Posterodorsally, a large branch may be traced through the parietal to open by two post-parietal foramina, and seems to correspond to the posterolateral sinus of Notoungulata (Patterson 1937). A deeper branch runs dorsally, internal to the parietal, to form the transverse sinus.

The transverse sinus meets its fellow in the mid-line whence the sagittal sinus passes forward between the cerebral hemispheres and the olfactory bulbs. The transverse sinus is connected to the jugular foramen by the lateral jugular sinus, which passes laterally to the cerebellar hemisphere, following the upper border of the periotic bone. A short canal from the lateral jugular sinus opens by the mastoid foramen between the occipital and periotic bones. Between the vermis and the hemisphere of the cerebellum, the transverse sinus gives off a second, smaller posterior branch, which passes down the posterior surface of the hemisphere, and joins the lateral jugular sinus near the jugular foramen. A fine vessel, perhaps an artery, can be seen in Rs 12a.32 and Rs 1.49 on the posterior surface of the vermis, passing up near the middle line.

The surface of the cerebral hemispheres shows several small vascular impressions. A vessel arising from the transverse sinus near the posterior end of the rhinal fissure gives off a number of small branches near its root; it is present in *Galerix*, *Neurogymnurus*, *Echinosorex* and *Erinaceus*, and appears to be the vena rhinalis posterior of Hofmann (1901). About half-way along the hemisphere, a vessel arises from the dorsal side of the lateral cerebral vein, and ramifies over the neopallium nearly to the mid-line; this occurs in all the erinaceid brain-casts examined, but Edinger does not mention it in her description of *Galerix*. In *Gymnurechinus* a posterior branch of this vein appears to anastomose with the vena rhinalis posterior. An anterior branch, also present in *Echinosorex*, runs parallel to the lateral cerebral vein and ends anteriorly in a faintly indicated transverse vein, which passes between the cerebrum and the olfactory bulb.

On the ventral surface, a prominence representing the inferior petrosal sinus passes forward from the jugular foramen. The carotid canal is situated in the suture between the periotic and the posterior sphenoid, at the side of the hypophysial fossa and a little posterior to the foramen ovale. More laterally in the same suture is the foramen spinosum for entry of the middle cerebral artery. A number of small transverse vascular channels cross the olfactory tract to the ventral surface of the pyriform lobe. As in *Erinaceus* and *Echinosorex*, a small vessel penetrates the frontal from the orbit and passes up the lateral side of the olfactory bulb to its dorsal surface.

THE OLFACTORY CHAMBER.—On Rs 1.49 the superficial bone was removed on the right side to expose the cast of the interior of the olfactory chamber (Text-figs. 5*a*, 5*b*; Pl. 1, figs. 7 & 8).

The olfactory chamber fills about half the length of the skull. It extends below the olfactory bulbs as far back as the suboptic foramen, where a venous canal passes through the anterior sphenoid immediately behind it. The total length of the olfactory chamber on the ventral side is thus nearly equal to the distance from the tip of the snout to the suboptic foramen: this is 58% of the total skull length, as in *Hylomys*; in *Echinosorex* it is 62% and in *Erinaceus* 65% (Table 11). As the variable length of the snout is included in these measurements, a truer picture is obtained if measurements are made from the infraorbital foramen instead of from the tip of the snout. This gives a result of 39–43% for *Gymnurechinus*, *Neurogymnurus*, *Hylomys*, *Echinosorex* and *Amphechinus*, as compared with 50% in *Hemiechinus auritus* and 56% in *Erinaceus europaeus*. The length of the olfactory chamber behind the infraorbital foramen is less than the width between the lachrymal foramina in *Hylomys* and *Amphechinus*, about one-eighth greater in *Gymnurechinus* and *Echinosorex* and 37% greater in *Erinaceus*.

The backward extension of the olfactory chamber between the orbits on the dorsal side is also greater in the Recent Erinaceinae than in *Gymnurechinus*. In *Gymnurechinus* the distance from the infraorbital foramen to the posterodorsal end of the olfactory chamber is 29% of the length of the skull behind the infraorbital foramen; in *Echinosorex* it is 36% and in *Erinaceus* 41%. In *Gymnurechinus*, also, the olfactory chamber extends only 2 mm. behind the postorbital process, whereas in *Hemiechinus auritus*, with a smaller skull, it extends 5·5 mm. behind the process. In Recent Erinaceinae the posterodorsal part of the chamber is indicated externally by a swelling on the frontal, but this is not so in *Gymnurechinus*, *Amphechinus* or *Neurogymnurus*; in *Echinosorex*, however, where the postorbital process is weakly developed, a slight swelling due to the olfactory chamber can be detected in this region.

As in *Erinaceus* and *Neurogymnurus* (Butler 1948), the olfactory chamber of *Gymnurechinus* is roughly triangular in cross-section, broader dorsally than ventrally. The greatest width across the turbinals is relatively less than in *Erinaceus*; it is 73% of the width between the lachrymal foramina, as compared with 93% in *Erinaceus*. The height of the posterior part of the chamber is also less than in *Erinaceus*: it is 77% of the distance between the lachrymal foramina in *Gymnurechinus* and 85% in *Erinaceus*. In *Gymnurechinus* the posterior height of the olfactory chamber is the same as the maximum height of the cerebrum; in *Erinaceus* it is 27% greater. The greater height of the olfactory chamber in *Erinaceus* affects the profile of the skull, which shows a characteristic rise above the orbits. In *Echinosorex*, *Neurogymnurus* and probably *Amphechinus* the relative width and height of the olfactory chamber resemble *Gymnurechinus* rather than *Erinaceus*.

The turbinal bones of *Gymnurechinus* seem to be similar in arrangement to those of *Erinaceus*. At the posterior end on the dorsal side is a chamber which must have contained the posterior concha of the nasoturbinal N1 (Butler 1948) and the medial concha of ectoturbinal N2 (1st secondary ethmoturbinal of Fawcett 1917). Lateral to this is a chamber for the lateral concha of N2 and the dorsal concha of N3 (2nd secondary ethmoturbinal of Fawcett); this occupies the most laterodorsal part of the olfactory chamber. Below this, on the side of the olfactory chamber, is a smaller space for the ventral concha of N3. The lower edge of this space marks the lower border of the recessus superior (lateral root of the 1st primary ethmoturbinal of Fawcett). Two turbinals follow, separated by rather narrow spaces: these are B1 (3rd secondary ethmoturbinal) and endoturbinal C (2nd primary ethmoturbinal). Below

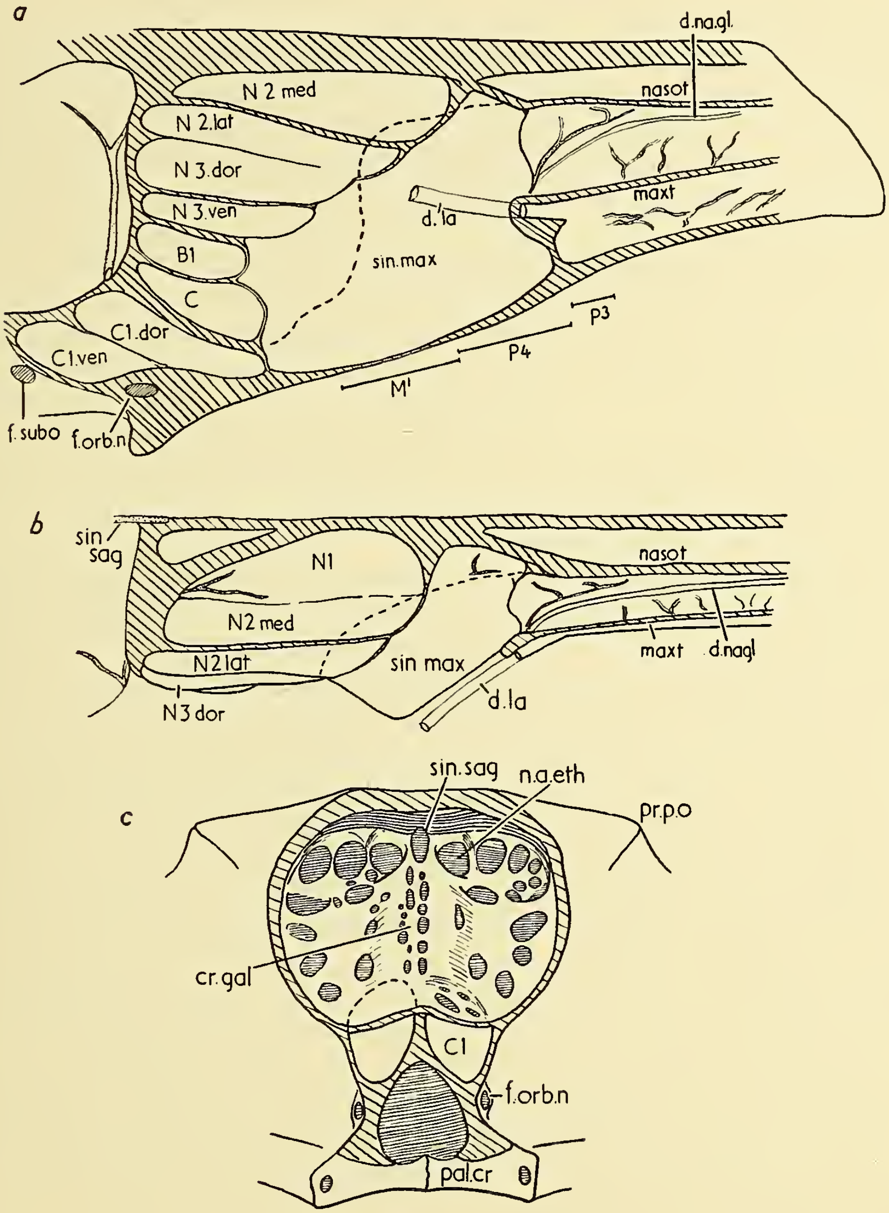


FIG. 5. *Gymnurechinus leakeyi*. (*a*), (*b*). Lateral and dorsal views of the cast of the olfactory chamber from Rs 1.49. ×4. The dotted line shows the posterior limit to which the chamber is lined by the maxilla. The positions of some of the teeth are shown. (*c*) Restoration of cribriform plate, from Rs 491.51 and Rs 623.50. ×4.

N 2 med.—C 1 ven., chambers for ethmoturbinals. *c.orb.n*, orbitonasal canal; *cr.gal*, crista galli; *d.la*, lachrymal duct; *d.na.gl*, impression of the duct of the lateral nasal gland; *f.orb.n*, orbitonasal foramen; *f.subo*, suboptic foramen; *maxt*, maxilloturbinal; *n.a.eth*, foramen for anterior ethmoid nerve; *nasot*, nasoturbinal; *pal.cr*, palatine crest; *pr.p.o*, postorbital process; *sin.max*, maxillary sinus; *sin.sag*, sagittal venous sinus.

this again is the space for ectoturbinal C1 (3rd primary ethmoturbinal), which extends back below the olfactory bulb.

In front of this series of ethmoturbinals is a sigmoid line which marks the posterior border of the maxillary sinus. The sinus reaches the hard palate medially to the roots of the teeth, and extends from near M^2 to near P^4, as in *Erinaceus*. Its greatest lateral extension is to a point just below the lachrymal foramen. The infraorbital canal passes through the maxilla immediately lateral to the sinus and dorsal to the roots of the teeth.

The attachment of the nasoturbinal may be seen running parallel to the median septum. The maxilloturbinal arises from the inner side of the maxilla in a curved line which begins at the upper surface of the hard palate above the anterior end of P^4, i.e. a little further forward than in *Erinaceus*. The line of attachment passes forward parallel to the palate in much the same way as in *Galerix*, whereas in *Erinaceus* it passes much higher up on the side of the respiratory passage. The lachrymal duct opens internally immediately below the maxilloturbinal, above P^3, as in *Galerix* and *Neurogymnurus*; in *Erinaceus* it opens above P^4. The lachrymal duct is therefore somewhat longer than in *Erinaceus*.

In the arrangement of the bones contributing to the wall of the olfactory chamber, *Gymnurechinus* resembles *Erinaceus*. The nasal is overlapped laterally by the maxilla. The frontal covers the greater part of the ethmoturbinal region and a small part of the maxillary sinus. More ventrally, the anterior sphenoid (to which the ethmoid is united) forms the lateral wall of the chamber for ectoturbinal C1, except for a small anterior part formed by the maxilla. Just below this chamber is the orbitonasal duct, which passes between the anterior sphenoid and the palatine.

The sagittal venous sinus continues forward into the olfactory chamber, passing between the frontals and the ethmoid as in *Erinaceus*. Between the nasoturbinal and maxilloturbinal some faint vascular impressions on the inner side of the maxilla show the position of the anterior part of the lateral nasal gland (Fawcett 1917). A more definite vascular impression passes back below the nasoturbinal and curves downwards posteriorly, receiving some small branches, to disappear near the anterior border of the maxillary sinus. In *Erinaceus*, an impression in the same position leads to a small foramen in the dorsal side of the lachrymal duct, and this is probably also true of *Gymnurechinus*. Running nearly parallel to this vessel is the impression of what seems to be the duct of the lateral nasal gland. A number of vascular impressions may be seen below the maxilloturbinal. Rs 623.50 and Rs 491.51 show foramina opening into the medial side of the infraorbital canal, probably as in *Erinaceus* and *Echinosorex*, for branches of the alveolar nerve.

CRIBRIFORM PLATE.—Rs 491.51 and Rs 623.50 have been prepared so as to show part of the cribriform plate from cranial view; from the two specimens the whole of the plate can be reconstructed (Text-fig. 5*c*). It is very similar to that of *Echinosorex*, and is less broadened than in *Erinaceus*. Dorsally there is a foramen for the sagittal venous sinus, and somewhat more ventrally there is on each side a foramen for the anterior ethmoidal branch of the profundus nerve. The crista galli is a slight convexity in the middle line; it is pierced by two series of small foramina communicating with the respiratory passage. On either side of the crista galli there is a convex area with few foramina, which roofs the respiratory passage. More laterally the cribriform plate is perforated by numerous foramina which open into the spaces between the turbinal bones.

In its orientation the cribriform plate may be regarded as consisting of three parts. The dorsolateral part, which forms the posterior wall of the recessus superior of the olfactory chamber, faces somewhat downwards in posterior view, so that the most anterior part of the olfactory bulb is at its lower edge. The most ventral part of the cribriform plate, behind the attachment of endoturbinal C, forms the roof of the chamber for turbinal C1, and is nearly horizontal. The remainder of the cribriform plate is inclined at an angle of about 45° to the basicranial axis.

UPPER TEETH.—*Gymnurechinus* has the typical erinaceine dental formula:

$$i\frac{3}{2},\ c\frac{1}{1},\ p\frac{3}{2},\ m\frac{3}{3}.$$

The root of I^1 is preserved in Rs 491.51, but the tooth is broken off at alveolar level. Rs 759.47 shows the basal half of the crown, but the very fragmentary nature of this specimen makes its reference to this species uncertain; it might belong to *Amphechinus rusingensis*. The cross-section of I^1 in Rs 491.51 is about $1{\cdot}8 \times 1{\cdot}6$ mm. at alveolar level, the length being a little greater than the breadth; in Rs 759.47 the cross-section is a little longer, measuring $2{\cdot}2 \times 1{\cdot}7$ mm. Rs 491.51 shows the stout root of I^1, 4·5 mm. in length, curving back above I^2 and I^3. The root of I^1 in *Erinaceus europaeus* is proportionately about the same size. The crown as preserved in Rs 759.47 differs from *Erinaceus* in its oval, rather than triangular, cross-section, the medial crest being very weakly developed.

To judge from the alveolus, the root of I^2 is much smaller than that of I^1, and is circular in cross-section. I^2 was evidently the smallest upper incisor, as in other Erinaceinae. It is in series with I^1 and I^3 and not displaced lingually as in many Recent Erinaceinae. Its root is inclined backwards, parallel to that of I^1.

I^3 is a larger tooth with two roots (seen in Rs 491.51), as in *Amphechinus* and some Recent Erinaceinae. The roots are close together and are inclined slightly backwards. The crown is unknown.

The canine is separated from I^3 by a diastema 1 mm. long in Rs 491.51. It has two somewhat divergent, stout roots. The crown is present in the holotype and in Rs 411.51, but in both specimens it is severely worn. The tooth resembles that of *Amphechinus edwardsi*, but in comparison with the width of the palate its alveolar length seems to be a little greater. Judging by the alveoli, the canine is appreciably larger than I^3.

P^2 is smaller than the canine, but it is less reduced than in *Amphechinus edwardsi*, and always has two roots. Its crown, which is visible in the holotype and in Rs 411.51, is lower than that of the canine, but resembles it in form.

The cheek teeth from P^3 backwards are badly worn in the holotype and Rs 491.51, but (except M^3) are well preserved in Rs 328.47, in which, though slightly larger, the teeth closely resemble the holotype in its proportions (Text-fig. 6; Pl. 4, fig. 33). The proportionate sizes of the cheek teeth are compared with those of *Amphechinus edwardsi* (measured on the photograph published by Viret 1929, pl. 1, fig. 2*d*) and *Erinaceus europaeus* in Tables 5 and 6, in which the measurements of the teeth are reduced to percentages of the width of the palate across the anterior part of M^1 and of the buccal edge of P^4. These tables show that *A. edwardsi* differs from *Gymnurechinus* and *Erinaceus* in the reduced size of its molars, both in length and width; *G. leakeyi* and *A. edwardsi* resemble each other and differ from *Erinaceus* in the greater buccal length of P^4; the molars of *G. leakeyi* are wider in proportion to the palatal width than those of *Erinaceus europaeus*; M^1 is approximately equal in proportionate length in *Gymnurechinus* and *Erinaceus*, but M^2 is slightly shorter in *Gymnurechinus*, especially across the middle of the crown.

P^3 is a triangular tooth with three roots. It is placed close behind P^2 so that its lingual apex is in line with the lingual side of P^2, and it projects beyond P^2 on the buccal side. The paracone is near the centre of the crown, and a metastylar crest runs to the posterobuccal apex, which is better developed than in most specimens of *Erinaceus*. There is a rudimentary parastyle, and the lingual part of the crown is occupied by a low but distinct protocone.

P^4 is quadrangular in outline, with a prominent posterobuccal apex, and is supported on three equal roots. The paracone is high; there is a well-developed metastylar crest; the parastyle is rudimentary, and there is no buccal cingulum. The lingual region bears a protocone, immediately lingual to the paracone, to which it is connected by a transverse crest; behind it is a much lower hypocone. P^4 closely resembles that of *Erinaceus*, and differs from *Amphechinus* in the greater development of the lingual region, so that the anteroposterior diameter across the waist of the crown is greater in proportion to the buccal edge.

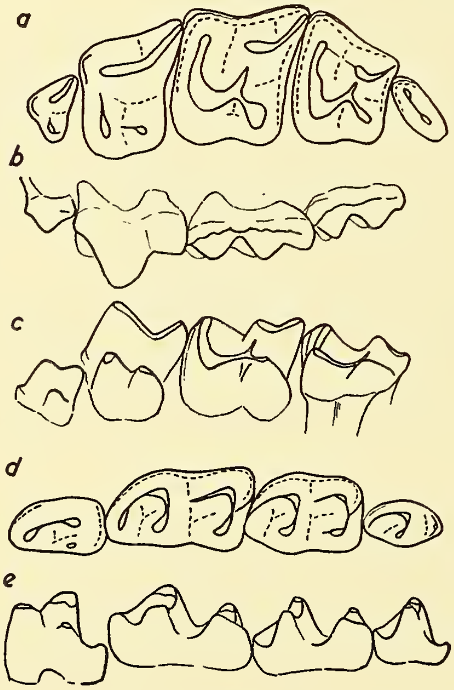


FIG. 6. Teeth of *Gymnurechinus leakeyi*. (*a*)–(*c*) P^3–M^2, crown, buccal and lingual views, Rs 828.47. In (*a*), M^3 has been restored. ×4. (*d*), (*e*) P_4–M_3, crown and lingual views, Rs 864.50. ×4.

M^1 is more transverse than in *Erinaceus*, and resembles that of *Amphechinus edwardsi* in proportions: the ratio, anterior width/buccal length, is 1·14. The paracone and metacone are divided by a deep groove to only a little above the level of the cingulum, whereas in *Erinaceus* the cusps join at a much higher level. Hürzeler's figure (1944, fig. 2) of *Amphechinus edwardsi* shows a condition very like *Gymnurechinus*. The buccal cingulum is always present; anteriorly it forms a small parastyle, from which a cingulum extends along the anterior edge of the crown. The metastylar shearing crest is well developed. The protocone is directly lingual to the paracone, and is connected to the bases of the paracone and metacone by crests. In the less worn M^1 of Rs 734.48 a metaconule can be seen on the posterior crest, similar to those of Recent Erinaceinae and evidently soon removed by wear. The hypocone is similar to that of *Erinaceus*, and is lower than the protocone. A posterior cingulum is present. There is usually no lingual cingulum, but in Rs 1006.50 a trace of it occurs between the bases of the protocone and hypocone. There are three roots; the lingual root is anteroposteriorly broadened and deeply grooved on the lingual side, as may be seen in Rs 1006.50.

M^2 also resembles that of *Amphechinus edwardsi* in general shape. The valley between the paracone and metacone is not so deep as on M^1, but still deeper than in *Erinaceus*. The metastylar crest, though present, is much shorter than on M^1; as in other Erinaceinae the buccal edge of the crown is oblique and the posterior edge is much shorter than the anterior edge. The hypocone is smaller in proportion to the protocone than on M^1. The development of the cingulum is much the same as on M^1; a trace of the lingual cingulum between the protocone and hypocone occurs in Rs 1006.50 and Rs 1.49. The lingual root is deeply grooved on its lingual side as in M^1.

M^3 is greatly simplified, as in other Erinaceinae. It is oval in outline and possesses two roots. The protocone is higher than the paracone, and there is no trace of a metacone or hypocone.

LOWER TEETH.—The crown of I_2 has not been preserved. The root, present in the holotype and in Rs 588.50, measures 2·0 × 1·4 in cross-section; its greatest diameter is therefore 20% of the alveolar length of M_{1-3}, as compared with 16–20% in Recent Erinaceinae and 23–28% in *Amphechinus* (Butler 1948, Table 1a). The root ends below P_2, in front of the mental foramen, and is thus about as long as in *Erinaceus europaeus* and *E. algirus* (Bohlin 1942, fig. 1); in *Amphechinus* the root of I_2 passes medially to the mental foramen and ends below P_4 (Bohlin 1942).

I_3, the smallest of the lower teeth, is known only by its alveolus. It is a procumbent tooth placed close behind I_2.

The alveolus of the lower canine, seen in the holotype and in 588.50, shows that it was a procumbent tooth, proportionately larger than in *Amphechinus edwardsi*. The alveolus measures 2·5 mm. in anteroposterior diameter, or about 70% of the alveolar length of P_4.

P_2 is preserved unworn in Rs 1971.50 (Pl. 2, fig. 16) and worn in the holotype. It is less reduced than in *Amphechinus edwardsi*, and possesses two parallel roots, which slope slightly backwards. The division of the root of P_2, while it occurs in *Neurogymnurus* and *Galerix*, is found among Erinaceinae only in *Gymnurechinus* and in

Amphechinus rusingensis, to be described below. In *G. leakeyi* the crown overhangs the root anteriorly, and possesses a main cusp, placed over the anterior root, and a small posterior basal cusp. Apart from the basal cusp, there is no cingulum. This tooth is narrower than in *Erinaceus*, and its main cusp is more conical. It tends to be placed somewhat obliquely in the jaw, so that its anterior root is more buccal than its posterior root, as may be seen in the holotype, Rs 1971.50, Rs 580.50 and Rs 930.50. A short diastema separates P_2 from P_4, as in other Erinaceinae.

P_4–M_2 are not well exposed in the holotype, but are preserved in Rs 864.50 (Text-figs. 6*d*, 6*e*; Pl. 2, fig. 15; Pl. 4, fig. 36). P_4 has a high trigonid and a small, cingulum-like heel, as in other Erinaceinae. The paraconid is only a little lower than the protoconid, but it is not so slender as in *Erinaceus*. As in *Amphechinus*, the trigonid of P_4 is relatively narrower than in Recent Erinaceinae, the paraconid being less displaced towards the lingual side. The metaconid is comparatively well developed: it is a distinct cusp, lower than the paraconid, and separated by a valley from the protoconid. There is no buccal cingulum.

M_1 is a relatively narrow tooth, due mainly to the development of the protoconid-paraconid crest, which is longer in proportion to the width of the crown and more longitudinal than in *Erinaceus*; the proportions of the tooth resemble those of *Amphechinus edwardsi*. The hypoconid of M_1 is about three-quarters of the height of the protoconid, as in *Erinaceus*, whereas in *Amphechinus* it is relatively lower. M_2 is also relatively narrower than in *Erinaceus*, the paraconid shearing crest being a little better developed; the hypoconid is as high in proportion to the protoconid as in *Erinaceus*. The roots of P_4, M_1 and M_2 are connected by a flange on the basal surface, which fits into a small groove in the bone between the alveoli, as in other Erinaceidae. M_3 resembles that of *Erinaceus*, except that the paraconid is more prominent anteriorly, as in *Amphechinus*, and a small heel is present, usually lacking in Recent forms. The root of M_3 is elongated anteroposteriorly, but is not divided.

In proportion to the length of M_1, P_4 is longer than in *Erinaceus* or *Amphechinus*, resembling in this respect *Neurogymnurus*. The proportionate length of M_2 to M_1 is the same as in *Erinaceus*, and greater than in *Amphechinus edwardsi*. M_3 is also less reduced in proportion to M_1 than in *Amphechinus* (Table 7).

ATLAS AND AXIS.—Part of the atlas is preserved in Rs 734.48 (Text-fig. 7). It has been broken through transversely, so that only the anterior portion remains.

The transverse process is much more strongly developed than in Recent Erinaceinae. It extends down the side of the arch, its anteroventral surface providing an extensive area of origin for the m. rectus capitis lateralis and the m. obliquus capitis superior; these muscles are inserted in the paroccipital process and the posterior lambdoid crest of the skull. On the anterior side of the transverse process is the anterior opening of the vertebrarterial canal; more ventrally is a pit for the origin of the m. rectus capitis anterior minor, which is inserted into the basioccipital near the jugular foramen. Dorsally, the upper edges of the articular facets are seen to project slightly in front of the arch; the neural spine appears to be weak. The canal for the first spinal nerve is visible on the broken posterior surface.

The axis is represented only by the odontoid process which is more slender than in Recent Erinaceinae, and resembles that of *Echinosorex*.

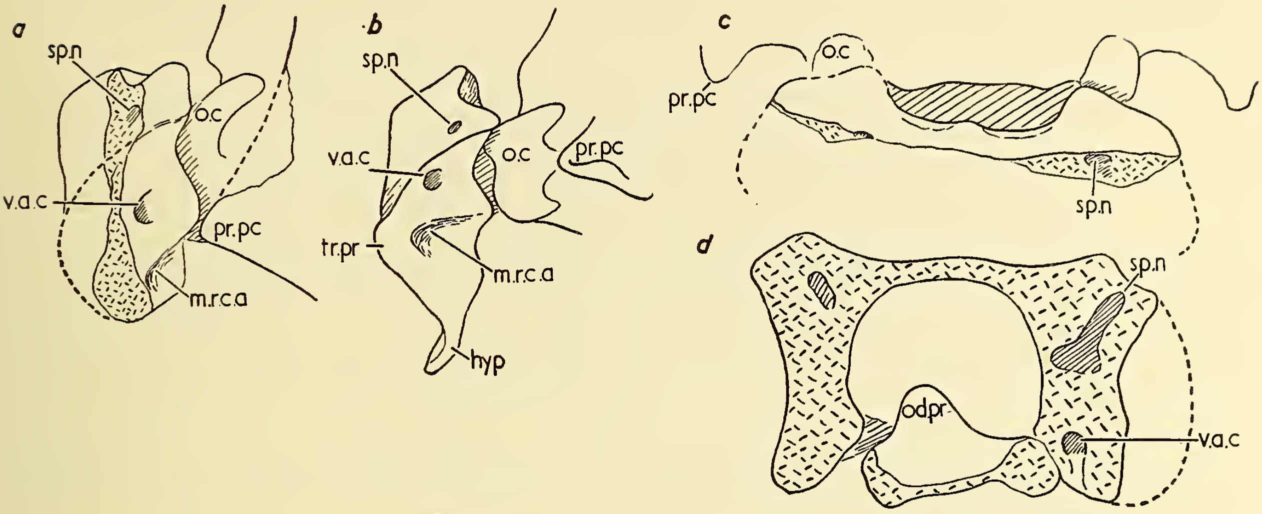


FIG. 7. (*a*), (*c*) and (*d*). Lateral, dorsal and posterior views of the atlas and adjacent structures, *Gymnurechinus leakeyi*, Rs 734.48, ×4, with (*b*) lateral view of the atlas and part of the skull of *Echinosorex gymnurus*, ×2·4.

hyp, hypapophysis; *m.r.c.a*, origin of rectus capitis anterior minor; *o.c*, occipital condyle; *od.pr*, odontoid process of the axis; *pr.pc*, paroccipital process; *sp.n*, canal for spinal nerve; *tr.pr*, transverse process; *v.a.c*, vertebrarterial canal.

RELATIONSHIPS.—In most features of the skull, *Gymnurechinus leakeyi* resembles the Echinosoricinae, *Neurogymnurus* and *Amphechinus* rather than the Recent Erinaceinae. Among these features may be enumerated:

1. Facial region long.
2. Prelachrymal flange well-developed; lachrymal foramen opening into the orbit.
3. Zygoma horizontal; condyle of lower jaw low; anterior edge of coronoid process oblique.
4. Suboptic foramen opening anteriorly to the sphenorbital foramen, and visible in lateral view.
5. Alisphenoid canal normally present.
6. Basiphenoidal pit absent.
7. Tympanic chamber resembling that of *Neurogymnurus*: alisphenoid forms about half its roof; upper border of external auditory meatus formed entirely from squamosal; tympanic process of alisphenoid not interrupted by the postglenoid foramen.
8. Characteristic form of the occipital condyle.
9. Olfactory chamber relatively smaller than in Recent Erinaceinae.
10. Petrosal lobe of the paraflocculus well developed.

These must be regarded as primitive characters of the family Erinaceidae. They are therefore of little value in assessing the special relationships between the genera.

Gymnurechinus also possesses a number of primitive characters which have been lost in some of the other genera:

11. Palatal vacuities rudimentary; they are better developed in some specimens of *Amphechinus* and in Recent Erinaceinae.
12. Lachrymal foramen above the anterior end of M^1, as in *Hylomys*, *Galerix*, *Neurogymnurus* and Recent Erinaceinae; in *Amphechinus* it is further forward, in *Echinosorex* and *Podogymnura* further back.
13. Overlap of parietals over frontals is comparatively slight, so that the fronto-parietal suture is approximately transverse, unlike *Hylomys* and *Neotetracus*.
14. Interparietal semicircular, as in *Hylomys* and *Neotetracus*; in *Echinosorex* and *Neurogymnurus* it is triangular, in *Amphechinus* and Recent Erinaceinae transverse.
15. Exposure of orbitosphenoid as in *Hylomys*, *Neurogymnurus* and *Amphechinus*; it is more elongated in *Echinosorex*, and reduced by overlap of the maxilla and alisphenoid in Recent Erinaceinae.
16. Zygoma without ventral process, as in *Hylomys*, *Neurogymnurus* and *Amphechinus*; the process is present in *Echinosorex* and the Recent Erinaceinae.
17. Anterior lambdoid crest and lambdoid triangle well developed, as in Echinosoricinae, *Amphechinus* and Recent Erinaceinae; unlike *Neurogymnurus*.
18. Tympanic bone probably moderately broad, as in most Erinaceidae; in *Echinosorex* it is very narrow.
19. Postorbital processes strong; skull markedly narrowed behind them; the processes are weak in *Echinosorex* and Recent Erinaceinae, and the midcranial region is relatively broad in *Hylomys* and the Recent Erinaceinae.
20. A few features of the dentition are relatively primitive: the canines are somewhat enlarged, and P_2 has two roots.

Gymnurechinus agrees closely with *Echinosorex* in the shape of its brain, which is more elongate than in *Neurogymnurus*, the Recent Erinaceinae and (judging by the skull) *Amphechinus*. An elongate brain also occurs in *Hylomys* and *Neotetracus*. However, in *Galerix*, which is usually regarded as a primitive member of the Echinosoricinae, the brain is short, and closely resembles that of *Neurogymnurus*. It would seem probable, therefore, that elongation of the brain is a character which has developed within the sub-family Echinosoricinae, and is not a primitive erinaceid character. *Gymnurechinus* also shares with *Echinosorex* a high occipital crest and a strongly constructed occipital surface of the skull: these characters appear to be adaptations to a powerful neck musculature, and are not present in *Hylomys*, which probably represents the more primitive condition. Other characters shared by *Gymnurechinus* and the Echinosoricinae appear to be primitive characters, as listed above. The resemblances to *Echinosorex* in brain-proportions and in the occipital crest are probably due to parallel evolution.

Apparently specialized features shared with *Neurogymnurus* are: the sculptured surface of the bone over the area of origin of the temporal muscle, though this is somewhat different in detail; the structure of the sagittal crest; the exposure of the mastoid on the side of the skull; the strong posterior lambdoid crest, which is continuous with the occipital crest; the high occipital crest; the structure of the region between the stylomastoid foramen and the paroccipital process. Against these are a number of differences. *Neurogymnurus* is more specialized in the modification of the anterior lambdoid crest and reduction of the lambdoid triangle; *Gymnurechinus* is more specialized in the elongate brain, and in the dentition.

Gymnurechinus shows special resemblance to *Proterix* in that the nasals extend back as far as the post-orbital processes.

The relationship of *Gymnurechinus* to the Erinaceinae shows most clearly in the dentition. Essentially erinaceine characters are: I^1 enlarged; I^2 greatly reduced; I^3 with two roots; P^1 absent; P^3 reduced in size but triangular; M^3 with only two roots, lacking a metacone; I_1 absent; I_2 enlarged; I_3 reduced; P_1 and P_3 absent; P_4 with elevated paraconid; talonid of M_3 rudimentary. In addition to these, *Gymnurechinus* shares with *Amphechinus* a number of characters of the teeth which are not present in Recent Erinaceinae, and are probably primitive for the Erinaceini: P^3 and P^4 are longer than in Recent forms, in proportion to the width of the palate; M^1 is more transverse; on M^1 the paracone and metacone are separated almost to the level of the cingulum; P_4 and M_1 are relatively narrow, with paraconids more directly anterior to the protoconids; the paraconids of M_2 and M_3 are less reduced than in *Erinaceus*; the talonid of M_3 is still present as a vestige.

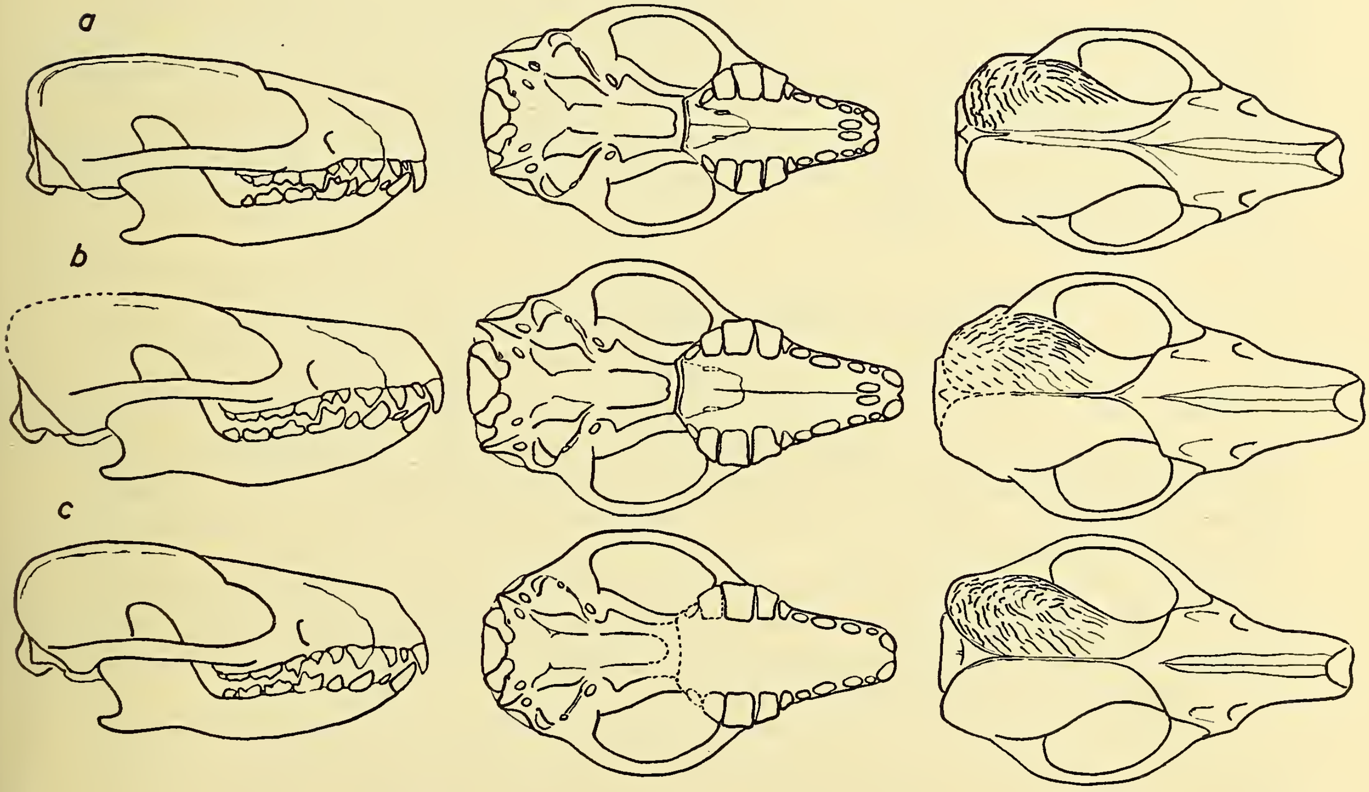


FIG. 8. Restorations of skulls of (*a*) *Gymnurechinus leakeyi*, (*b*) *G. camptolophus*, (*c*) *G. songhorensis*. Natural size.

Gymnurechinus also shares with *Amphechinus* the high occipital crest, the consolidated occipital surface of the skull, and the low foramen magnum, which does not rise above the condyles; these features, seen also in *Echinosorex* and *Neurogymnurus*, indicate a strong neck musculature. In the sculptured surface of the temporal region, *Gymnurechinus* is more like *Amphechinus* than *Neurogymnurus*. The extension of the mastoid exposure anterior to the lambdoid crest is found in *Amphechinus* and *Neurogymnurus* as well as in *Gymnurechinus*.

Gymnurechinus has avoided the specializations which divide *Amphechinus* from the modern Erinaceinae. Its anterior incisors are less enlarged; the root of I_2 extends back only as far as P_2, whereas in *Amphechinus* it ends below P_4; the premaxilla is less elongated than in *Amphechinus*; the sagittal crest is not so high; the cheek teeth are not displaced so far backward beneath the orbit; the molars are less reduced in size; the lingual part of P^4 is better developed; the metaconule is always present on unworn M^1 and M^2; the metaconid is always present on P_4; the mid-cranial region is less shortened. In these respects *Gymnurechinus* is nearer to *Erinaceus*.

At the same time *Gymnurechinus* possesses characters which exclude it from the ancestry of *Erinaceus*: the elongation of the brain and cranium; the position of the lateral cerebral vein in relation to the rhinal sulcus; the specializations of the back of the skull, which are found also in *Neurogymnurus*.

Gymnurechinus leakeyi therefore represents an extinct sideline within the Erinaceini. Since *Amphechinus* can be traced back to the Stampian, its common ancestor with *Gymnurechinus* could not have lived later than the Lower Oligocene. The presence of *Gymnurechinus* in the Lower Miocene is evidence for the existence of Oligocene Erinaceini which did not develop the specializations of *Amphechinus*. Such hypothetical forms might well have given rise to the modern hedgehogs, which would have branched off from the *Gymnurechinus* line before the specializations of *G. leakeyi* had been developed.

Gymnurechinus camptolophus sp. nov.

(Plate 2, figs. 9–11, 17, Pl. 4, fig. 35; Text-figs. 8*b*, 9*b*, *e*, 10–14)

DIAGNOSIS.—A species of *Gymnurechinus* that differs from *G. leakeyi* in the following characters: face larger in proportion to the cranium; sagittal crest sharp; occipital condyles broader at their dorsal ends; M^1 and M^2 less transverse; P^4 with reduced hypocone. Width of palate across paracones of first molars 18·7 mm., alveolar length of M_1–M_3 11·0–11·4 mm.

HOLOTYPE.—Rs 424a.48, skull from sub-site R 105A, west of Kiahera, Rusinga Island. The anterior part is well preserved, and shows unworn teeth back to P^4; the posterior part is crushed and part of the posterodorsal surface is missing. The specimen is broken transversely into three pieces.

REFERRED MATERIAL.—The holotype was found in a small pocket about 4 ft. × 3 ft. × 1 ft. thick, which also contained other specimens referable to the same species, together with scattered bones, jaws and teeth of a large number of other mammals, including small antelopes, rodents and small carnivora. The following specimens are referred to *G. camptolophus*:

Rs 424.48. A skull, jaw and the greater part of a skeleton, many of the bones of which are still articulated. The skull agrees in measurements with the holotype, but represents an older individual, the teeth being considerably worn.

Rs 424b.48. Isolated unworn teeth: right and left M^1, right M^2, the talonid of left M_1, and the trigonid of left M_2. The unworn condition of these suggests that they belong to the same individual as the holotype.

Rs 564.48 and Rs 212.48. Two incomplete lower jaws, with unworn teeth back to P_4, again probably representing the same individual as the holotype.

Rs 595.48. A fragment of lower jaw with lightly worn P_2 and P_4, agreeing closely in size with Rs 564.48, but the ramus somewhat deeper.

Rs 424c.48. The numerous skeletal fragments found near the holotype include three humeri, all incomplete, which agree with the humerus in Rs 424.48. Other bones, such as fragments of phalanges, and the head of a left femur, might also belong to the same species, but cannot be identified with any probability.

The following fragmentary specimens from other sites are referred to this species:

Rs 1394.50, from Kathwanga. The tip of a snout with the roots of I^1–C. It is larger than *G. leakeyi* (491.51), but a little smaller than the holotype of *G. camptolophus*.

Rs 366.49, from Kamathangere (near sub-site R 113). The tip of a lower jaw with I_3–P_2, resembling Rs 564.48 but a little smaller.

Rs 145.41, from an unknown site on Rusinga Island. A fragment of jaw with worn M_1, larger than *G. leakeyi* and agreeing in size with Rs 424b.48 and Rs 564.48.

Rs 732.47, from Hiwegi, sub-site R 3. A fragment of jaw with badly worn and broken M_1 and P_4, agreeing as far as can be seen with Rs 145.41.

Like *G. leakeyi*, this species has been found only on Rusinga. With one exception, all the specimens have been obtained from the western side of the island, whereas the majority of specimens of *G. leakeyi* were found in the Hiwegi Series on the eastern side. The two species are so closely related that fragments of jaws are usually to be distinguished only by the rather unsatisfactory criterion of size, but the difference of distribution indicates a difference of geological age: *G. camptolophus* appears to occur a little later than *G. leakeyi* and is probably descended from it.

THE SKULL.—The facial region of the skull is appreciably longer and wider than in *G. leakeyi*: compared with Rs 491.51, the length of the palate in the holotype is 18% greater and its width 14% greater (Pl. 2), while the zygomatic width of Rs 424.48 is 17% greater than in the holotype of *G. leakeyi*. On the other hand, measurements of the cranium show less difference between the two species: the length of the skull behind the palatal crest is only 6% greater than in the holotype of *G. leakeyi*, and the postglenoid width, though affected by crushing, seems to be approximately the same in the two species. The face is thus larger in proportion to the cranium in *G. camptolophus* than in *G. leakeyi* (Table 2; Text-figs. 8*a*, *b*).

The nasals extend back as far as in *G. leakeyi*. In the holotype, the extra-nasal processes of the premaxillae do not meet the frontals, so that the nasal makes contact with the maxilla over a length of 3·5 mm.; this, however, is probably due to the youth of the specimen, as in Rs 424.48 the premaxillae meet the frontals exactly as in *G.*

leakeyi. The anterior edge of the orbit resembles that of *G. leakeyi.* Most of the zygoma is missing in the holotype, but in Rs 424.48 it agrees closely with *G. leakeyi.*

The sagittal crest is narrower than in *G. leakeyi,* and triangular in cross-section instead of being flattened at the top. There is also a slight difference in the lambdoid triangle, because the anterior lambdoid crest meets the auditory meatus a little further away from the mastoid process than it does in *G. leakeyi.* The area of origin of the temporal muscle is ridged as in *G. leakeyi,* but the ridges extend over the parietal nearer to the sagittal crest. Other features of the skull roof are as in *G. leakeyi.*

In the holotype the palate is damaged posteriorly, but vacuities, if present, must have been small. The hard palate ends shortly behind the palatal crest. The orbitotemporal region resembles *G. leakeyi.* An alisphenoid canal is present. The tympanic chamber is well preserved in the type, and agrees closely with *G. leakeyi*: the only difference noticed is the more transverse development of the recessus meatus (Text-fig. 9*b*). Although the tympanic process of the basisphenoid is completely preserved, there is no trace of the tympanic bone or of ear-ossicles. The medial flange of the tympanic process, foreshadowing the posterior margin of the basisphenoid pit, can be seen. The crest which connects the paroccipital process to the mastoid process is somewhat more emarginated for the hyomandibular nerve than in *G. leakeyi.*

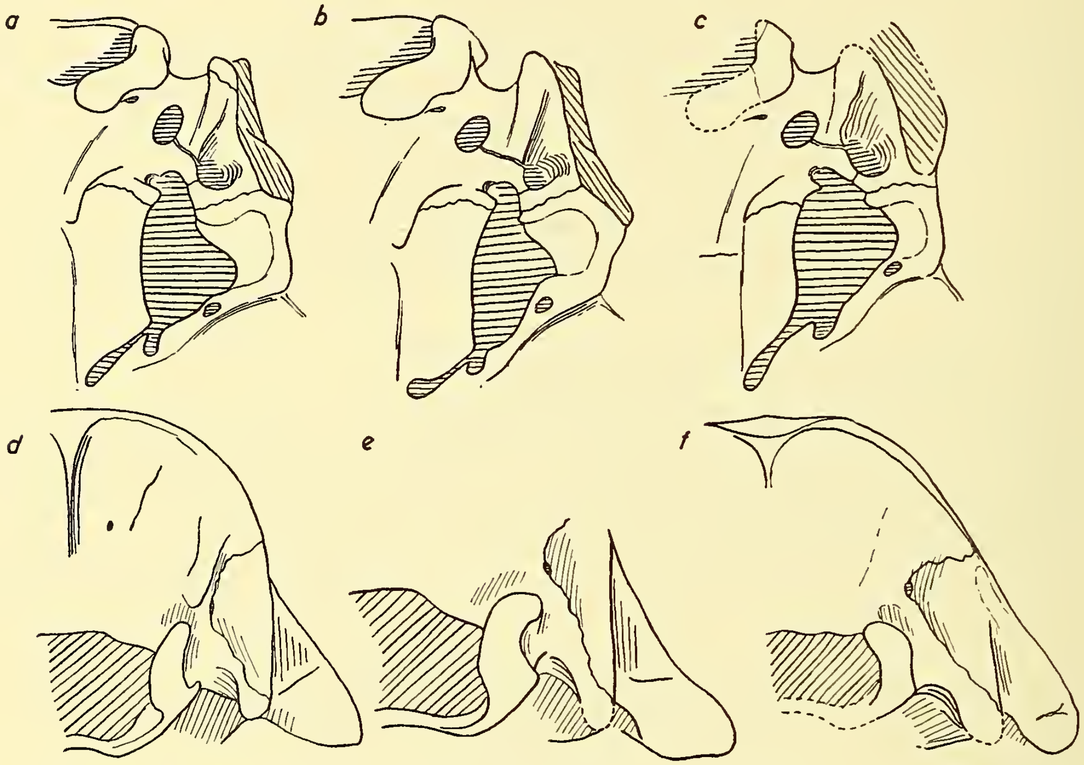


Fig. 9. Ventral and posterior views of the posterolateral part of the skull. (*a*), (*d*) *Gymnurechinus leakeyi.* (*b*), (*e*) *G. camptolophus.* (*c*), (*f*) *G. songhorensis.* Drawn from the holotypes. × 3.

The occipital condyles (Text-figs. 9*b*, *e*) are more prominent than in *G. leakeyi,* so that the notch between the paroccipital process and the condyle is deeper. The most dorsal part of the condyle is more expanded towards the lateral side. The median crest on the occipital bone is well developed in Rs 424.48; traces of it are visible in the holotype, in which the greater part of the occipital surface is broken away.

Some features of the interior of the skull are visible in the holotype. Owing to breaking away of part of the skull roof, a small part of the cast of the lateral cerebral vein can be seen in a similar position to that of *G. leakeyi*. The specimen is broken transversely just behind the orbits, permitting the removal of some of the matrix from the anterior part of the cranial cavity (Text-fig. 10*a*). As in Recent Erinaceidae, the anterior sphenoid forms a transverse strut across the floor of the cranial cavity behind the olfactory bulbs and the optic nerves pass almost directly forwards through it. In the middle line the anterior sphenoid rises to a blunt keel, separating the ventral parts of the olfactory bulbs; this keel is much better developed than in *Erinaceus* or *Echinosorex*.

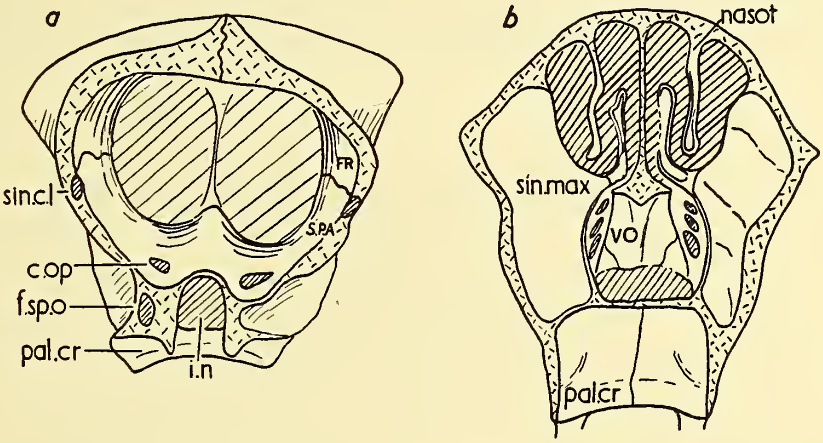


Fig. 10. Two cross-sectional views of the holotype skull of *Gymnurechinus camptolophus*. (*a*) Looking forwards into the anterior end of the brain-cavity. (*b*) Section through the olfactory chamber, looking backwards. × 3.

c.op, canal for optic nerve; *f.sp.o*, sphenorbital foramen; *i.n*, internal nares; *nasot*, nasoturbinal; *pal.cr*, palatine crest; *sin.c.l*, lateral cerebral sinus; *sin.max*, maxillary sinus (posterior wall exposed on the right side of (*b*)); *vo*, vomer.

A clean fracture across the face exposes a section through the olfactory chamber (Text-fig. 10*b*). About 2·5 mm. above the false palate is a keeled bone in the true palate, agreeing closely with the posterior end of the vomer of *Erinaceus*. Lateral to this is a slit-like opening which leads to the olfactory chamber. On the lateral side of this slit may be seen three openings, which occur also in *Erinaceus* (Parker 1885, pl. **81**, fig. 8). In *Erinaceus* the most posterior of these openings leads to the space behind endoturbinal C; next anteriorly is an opening between endoturbinals C and B, and in front of this an opening between B and A. The number of endoturbinals in *Gymnurechinus* therefore was probably the same as in *Erinaceus*. The most posterior opening is above the anterior part of M^2, as in *Erinaceus*. More dorsally, the nasoturbinal (processus uncinatus) is seen in section, at the side of the median septum.

Passing below its edge and up its median side is the anterior spur of endoturbinal A. The more lateral part of the fracture shows the posterior wall of the maxillary sinus, which is marked by impressions of the ethmoturbinals behind it to a greater extent than in *Erinaceus*.

UPPER TEETH.—The anterior teeth are better known than in *G. leakeyi*, being well preserved in the holotype (Text-fig. 11; Pl. 2, figs. 10 & 11). The tip of I^1 has been broken off, but enough remains of the crown to show that it is more vertical than in *Erinaceus*. In cross-section it is roughly triangular, thus resembling *Erinaceus* rather than *G. leakeyi* (Rs 759.47). There is a short diastema between I^1 and I^2 as in *G. leakeyi*. I^2 has a high, conical crown, more vertical than in *Erinaceus*; anteroposteriorly it is shorter than in *Erinaceus*, and does not possess a posterior basal cusp. I^3 is also more vertical than in *Erinaceus*; it is much higher than I^2, and has two roots which are more widely separated than in *G. leakeyi*. It differs from I^3 of *Amphechinus edwardsi* in the weaker development of the posterior basal cusp. Between I^3

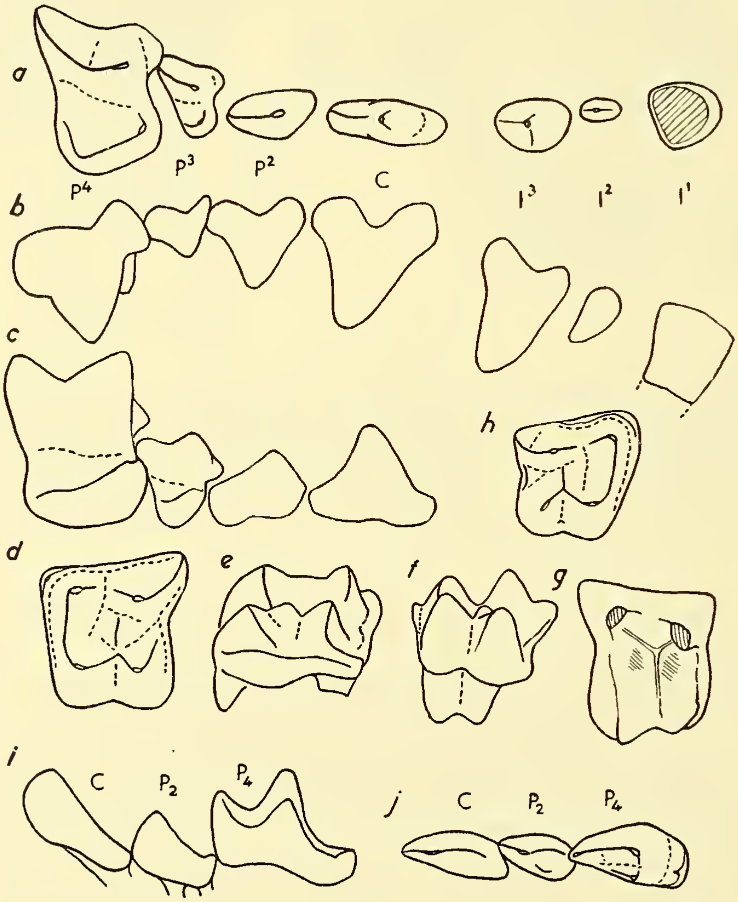


FIG. 11. *Gymnurechinus camptolophus*. (*a*), (*b*) and (*c*) Antemolar teeth of the holotype, in crown, buccal and lingual views. (*d*), (*e*), (*f*) and (*g*) M^1, Rs 424b.48, crown, posteroventral, lingual and basal views. (*h*) M^2, Rs 424b.48, crown view. (*i*), (*j*) Lower antemolar teeth of Rs 564.48, lingual and crown views. ×4.

and the canine is a diastema about 2 mm. long. The canine is higher than I^3, and much longer; in crown view it seems to be longer in proportion to its width than in *G. leakeyi*, but this may be due to the small degree of wear. The crown is mainly occupied by a vertical, trenchant cusp, and there is an anterior basal cusp in addition to the posterior basal cusp seen in *G. leakeyi*. P^2 is placed immediately behind the canine: it is shorter and less elevated, its basal cusps are less distinct, and there is a lingual convexity of the outline which foreshadows the development of the lingual lobe. Both the canine and P^2 have two roots.

P^3 resembles that of *G. leakeyi*. On P^4, however, the lingual part of the crown differs in the two species. There is a well-developed protocone near the anterior border; from the tip of this a crest passes back and then turns buccally, following the edge of the tooth; the hypocone is hardly distinguishable as a faint elevation of this crest. Such a reduced hypocone occurs among Recent Erinaceinae more frequently on Pd^4 than on P^4, but because of its large size, its transverse development, and its unworn condition, the tooth in Rs 424a.48 is almost certainly not a milk-molar. It resembles P^4 of *Paraechinus nudiventris* (B.M. Z.D. 88.6.18.7).

The molars are absent in the holotype, but unworn examples of M^1 and M^2 were found at the same site and may have come from the same individual, as they agree in size with the alveoli of the holotype (Text-fig. 11; Pl. 4, fig. 35). The molars are less transverse than in *G. leakeyi*: the ratio, anterior width of tooth/length of buccal edge is, for M^1, 1·02, against 1·14 in *G. leakeyi*, and for M^2, 1·13 against 1·31. On the unworn crown of M^1 it is possible to see that the metacone is a little higher than the paracone, and that a distinct metaconule is developed, resembling that of many specimens of Recent Erinaceinae. The hypocone is a little lower than the protocone, and possesses a distinct postero-buccal crest. There is no lingual cingulum. The alveolar view shows three crests from the roots, meeting in the middle of the basal surface, as in other Erinaceidae (Butler, 1948, figs. 12 & 25). The lingual root is deeply grooved on the lingual side, but is not divided. M^2 differs from M^1 in the reduction of the metastylar region, the smaller metacone, which is no higher than the paracone, the less distinct metaconule, and the smaller hypocone.

Except that M^1 and M^2 are less broad, the proportions and relative sizes of the cheek teeth of *G. camptolophus* agree very closely with those of *G. leakeyi* (Tables 4–6).

LOWER JAW.—The lower jaw is preserved in Rs 424.48, the horizontal rami of younger specimens in Rs 564.48 and Rs 212.48, and the anterior end in Rs 595.48 and Rs 366.49. No difference from *G. leakeyi* can be detected except the greater size (Table 3).

LOWER TEETH.—The anterior teeth are best preserved in Rs 564.48 (Text fig. 11; Pl. 2, fig. 17), Rs 212.48, Rs 595.48 and Rs 366.49. The crown of I_2 is missing in all these specimens. Dissection of the jaw of Rs 212.48 shows that the root, which is 2·2 mm. in greatest diameter, extends back almost to the posterior end of P_2. I_3 is known only in Rs 366.49; it is a small, procumbent tooth, the crown projecting forwards beyond the single root and overhanging the posterior end of I_2. The low main cusp is placed well forward on the crown; from it there run a short anterior crest and a less distinct posterior crest, displaced towards the buccal side. The lingual part of the crown is occupied by a rounded cingulum, which broadens postero-laterally to form a shallow basin. The canine is similar in shape to I_3 but much larger: it is nearly twice as long as I_3, and longer than P_4, and is thus relatively larger than in *Amphechinus* and *Erinaceus*. P_2 possesses two roots, but its crown is more elevated than in *G. leakeyi*, especially in Rs 564.48, in which the tip of P_2 is almost as high as the paraconid of P_4.

P_4 in Rs 564.48 and Rs 212.48 has a distinctive appearance owing to the slender, comparatively low paraconid, which is separated from the protoconid by a deep incisure. It resembles Pd_4 of some Recent forms. The protoconid is more vertical, and does not show the inward and posterior inclination which is usual in *G. leakeyi*. The tooth measures 3·9×2·3 mm. Rs 595.48 approaches *G. leakeyi* in its stouter paraconid, but the incisure between the paraconid and protoconid is still deep.

An isolated talonid of M_1 from the same site as the holotype shows no differences from *G. leakeyi* except its larger size. The crest on the anterior side of the root is clearly visible. A trigonid of M_2 from the same site also resembles *G. leakeyi* except in size. The mandible fragment Rs 145.41 is referred to this species because its worn M_1 closely agrees in size with the isolated talonid from R 105a. It measures 5·2×3·3 mm. Rs 732.47 is in still worse condition, but shows no differences from Rs 145.41.

Post-cranial Skeleton.—The skeleton (Rs 424.48) has undergone considerable disturbance before fossilization. The skull and the vertebral column as far back as the third sacral vertebra remain in articulation, together with most of the ribs and part of the right innominate bone. The back is bent dorsally in the region of the neck and anterior thoracic vertebrae, and ventrally at the posterior end of the thorax. The thorax has been crushed laterally, and most of the ribs are broken. The limbs have suffered most disturbance. The right femur is detached from the pelvis and lies across the ribs; the right tibia is still further forward, near the anterior end of the thorax, while the left tibia lies parallel to the sacrum. The upper end of the humerus and most of the scapula are missing, but the lower end of the right humerus is approximately in its natural position and near it is a small fragment of the ulna. Apart from a metatarsal and a phalanx lying near the anterior part of the thorax, nothing can definitely be referred to the skeleton of the feet, and there is no trace of the tail. A number of isolated bones in the same block of matrix have been omitted from the following description, because there is no evidence of their erinaceid character; among them is the jaw of a rodent.

vertebral column.—In Rs 424.48 the vertebral column is preserved as far back as the third sacral vertebra. The vertebral formula is *C.* 7, *Th.* 14, *L.* 6, *S.* 3+?, *Cd.*?. The length of the body, from the occipital condyle to the acetabulum, is estimated as 14 cm.: this is slightly less than in *Erinaceus* (*Atelerix*) *algirus* (15·5 cm.) and *E. europaeus* (17 cm.), skeletons of which were measured.

The atlas (Text-fig. 12*a*, 12*d*) resembles that of *Echinosorex* rather than the Recent Erinaceinae in the relatively great anteroposterior diameter of the neural arch. The surface articulating with the occipital condyle is more concave than in *Erinaceus*, and its dorsal edge projects forward more than in *G. leakeyi*, so that the anterior edge of the arch above the articular surface is further removed from the foramen of the first spinal nerve (3·6 mm., compared with an estimated 2·5 mm. in *G. leakeyi*). This is in accordance with the greater development of the dorsal part of the condyle in *G. camptolophus*. The transverse process of the atlas is incompletely preserved, but it evidently formed a well-developed oblique flange, its somewhat concave

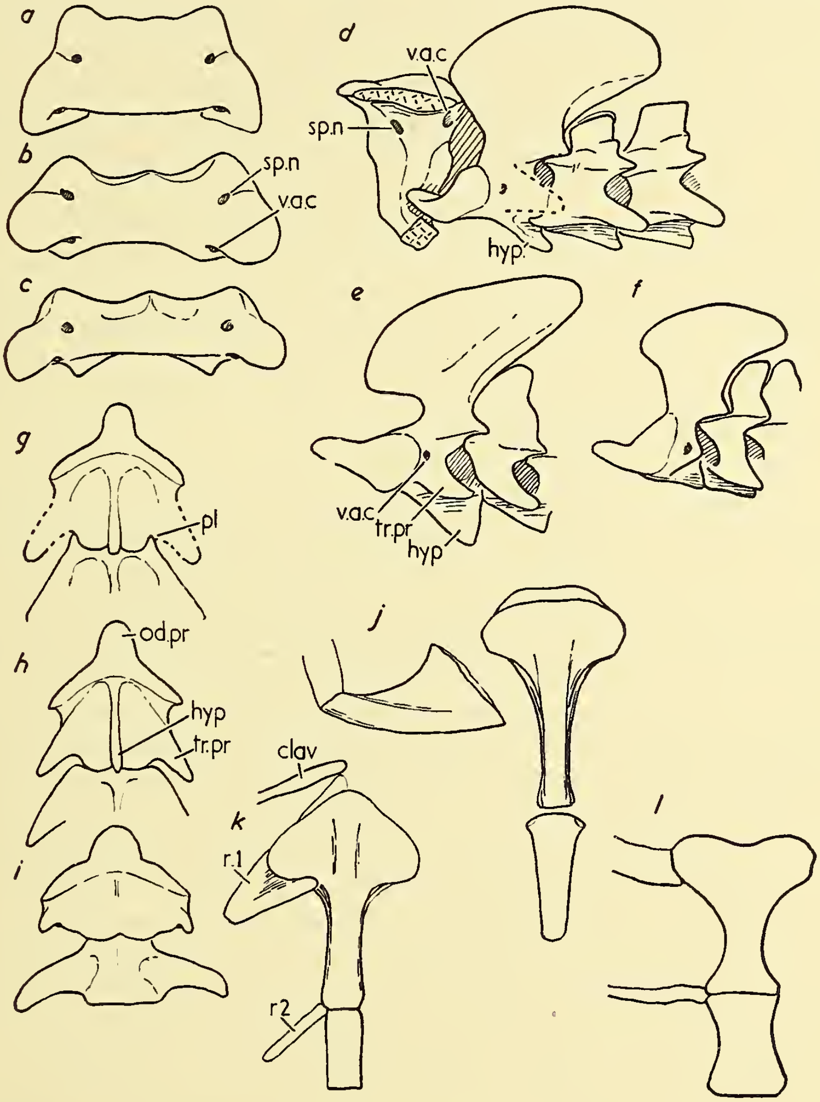


Fig. 12. *Gymnurechinus camptolophus*. (*a*) Atlas, dorsal view. (*d*) Anterior cervical vertebrae, side view, the atlas seen in medial view. (*g*) Axis and third cervical, ventral view. (*j*) Manubrium sterni, possible xiphisternum, and lower end of first rib, ventral view. All from Rs 424.48. ×2.

Echinosorex gymnurus. (*b*) Atlas, dorsal view. (*e*) Axis and third cervical, lateral view. (*h*) Axis and third cervical, ventral view. (*k*) Manubrium sterni and adjacent structures, ventral view. ×1·4.

Erinaceus europaeus. (*c*), (*f*), (*i*) and (*l*) The same structures, for comparison. ×2.

clav, clavicle; *hyp*, hypapophysis; *od.pr*, odontoid process; *pl*, pleurapophysis; *r*. 1, *r*. 2, lower ends of first two ribs; *sp.n*, foramen for spinal nerve; *tr.pr*, transverse process; *v.a.c*, opening of vertebrarterial canal.

posterodorsal surface providing an extensive insertion for the m. obliquus capitis inferior. The ventral part of the atlas shows pits for the origin of the mm. rectus capitis anterior minor et lateralis, as in *G. leakeyi*. The atlas differs from that of *Echinosorex* in the absence of a hypapophysial spine.

The axis (Text-fig. 12*d*, 12*g*) also resembles that of *Echinosorex* rather than that of *Erinaceus*. There is a large, hatchet-shaped spine, 14 mm. long and 8 mm. high: in *Erinaceus europaeus* the spine is 9 mm. long and 5 mm. high. Its upper edge is more evenly curved than in *Echinosorex*, and the notch below its anterior end is less deep. The greater part of the spine is roughened for the origin of the m. obliquus capitis inferior, and near the posterior border is a hollow for the insertion of transverso-spinalis muscles. The odontoid process is longer than in *Erinaceus*, and resembles *Echinosorex*, except that it turns upwards at its tip as in *Erinaceus*. The transverse process is broken, but its pointed tip is preserved, showing that it was better developed than in Recent Erinaceinae. The upper edge of the posterior zygapophysis forms a longitudinal crest for the origin of a slip of the m. semispinalis capitis, as in Recent Erinaceidae. The centrum is marked ventrally by a pair of depressions for part of the m. longus cervicis, separated by a median crest which, as in *Echinosorex*, terminates posteriorly in a hypapophysial spine.

C. 3 and *C*. 4 are more elongate than in Recent Erinaceinae, and resemble those of *Echinosorex*. The length diminishes to a minimum in *C*. 6–*Th*. 1. The neural spines of the cervical vertebrae are better developed than in Recent Erinaceinae. That of *C*. 3 is low, bifid, and overhung by the spine of the axis; on *C*. 4 the spine is single and approximately rectangular in side view; on *C*. 5 it is also rectangular, but shorter antero-posteriorly; on *C*. 6 it is still shorter antero-posteriorly, and inclined somewhat forwards; on *C*. 7 the spine is higher, especially posteriorly, and its antero-posterior diameter is much greater. The neural arch of *C*. 3 bears a prominence near a convexity of its posterior edge; slightly more laterally and anterior to this is another prominence (Text-fig. 12*d*). The more posterior prominence becomes progressively less distinct on the more posterior cervicals, and the convexity of the posterior border disappears on *C*. 6; the anterior prominence however remains, disappearing only on *Th*. 4. These prominences are found in Recent Erinaceidae, though less strongly developed: they serve for attachment of parts of the transverso-spinalis ("multifidus") musculature, the more posterior and median prominence giving insertion to a slip of the muscle passing backwards, and the more anterior prominence forming the origin of a small tendon which passes forward into the body of the muscle. On *C*. 3–7 a crest for the origin of a slip of the m. semispinalis capitis occurs above the posterior zygapophysis. Farther forward, another crest below the anterior zygapophysis probably gave rise, as in *Erinaceus*, to a slip of the m. longissimus atlantidis, which is inserted into the transverse process of the atlas. The two crests are almost continuous, but are separated on *C*. 3, and less distinctly also on the more posterior cervicals, by a groove for the dorsal branch of the spinal nerve. The transverse process of *C*. 3 is directed backwards, as in Recent Erinaceidae, below the anterior zygapophysis of *C*. 4. On its ventral side is a crest, which passes forwards and inwards, terminating anteriorly in a ventral pleurapophysis (Text-fig. 12*g*). A rudimentary pleurapophysis occurs on *C*. 3 in *Hemiechinus auritus*; in *Echinosorex* and in *Erinaceus algirus* it appears first on *C*. 4, and in *Erinaceus europaeus* on *C*. 5. In

Gymnurechinus, as in other Erinaceidae, the pleurapophysis of *C.* 6 is greatly enlarged, forming a ventral flange which extends back below *C.* 7. No pleurapophysis is present on *C.* 7. Each cervical vertebra behind the atlas has a median ventral crest, which terminates posteriorly in the hypapophysis. This is best developed on *C.* 3 and 4; it is somewhat shorter on *C.* 5, in which it is bifurcated at the tip. Hypapophyses are absent in Recent Erinaceinae, but well developed in Echinosoricinae.

The anterior thoracic vertebrae differ from those of Recent Erinaceinae in the height of the neural spines (Text-fig. 14). The highest spines are those of *Th.* 2 and 3, that of *Th.* 3 being the stoutest; the spine of *Th.* 4 is slightly lower, and the height diminishes gradually in *Th.* 5 and 6. These spines are somewhat better developed than in *Echinosorex.* The next visible spine is that of *Th.* 10, which resembles those of the lumbar vertebrae. A metapophysis begins to appear on *Th.* 3 as an elevation of the upper edge of the transverse process. It becomes progressively larger on *Th.* 4–7; in *Th.* 7–10 it is truncate at the tip, as in typical thoracic metapophyses of Recent Erinaceidae. The diaphragmatic vertebra (Slijper 1946) is *Th.* 11, as in *Hemiechinus auritus* and probably also *Hylomys* (Anderson 1874); in *Echinosorex* it is *Th.* 12, in *Erinaceus* and its sub-genus *Atelerix Th.* 13. The tubercular facet moves down the side of the vertebra towards the capitular facet from *Th.* 5 to *Th.* 12; on *Th.* 13 the tubercular facet is only doubtfully distinct. In the anterior thoracic vertebrae the ventral surface of the centrum is marked by a pair of depressions for slips of the m. longus cervicis posterior, separated by a median rounded keel, much as in *Echinosorex.* The median keel fades in *Th.* 6, and from *Th.* 7 backwards the ventral surface is evenly rounded, as in *Echinosorex*, but much less convex than in Recent Erinaceinae. At the sides of the ventral surface, lateral to the muscle depression, is a longitudinal crest, best developed on the more anterior thoracic vertebrae; on *Th.* 8 the more anterior part of this lateral keel has disappeared.

The posterior thoracic and lumbar neural spines (Text-fig. 13*a*) are nearly rectangular in side view, resembling those of *Echinosorex.* The stout, lumbar type of metapophysis appears on *Th.* 11. The anapophysis is well developed on *Th.* 12. On *Th.* 10 an oblique crest appears, passing back from the metapophysis to end below the posterior zygapophysis; on *Th.* 11 the anapophysis is just visible as a differentiation of this crest. On *Th.* 13 the crest is interrupted, its posterior part being represented by a horizontal flange passing forward from the anapophysis above the rib facet. A more ventral horizontal flange appears on *Th.* 10 behind the tubercular facet; it broadens on the lumbar vertebrae to become the transverse process, which appears to carry the anapophysis on its upper posterior edge. The transverse processes of the lumbar vertebrae are better developed than in *Echinosorex* or in Recent Erinaceinae, but resemble those of *Hylomys* (Anderson 1874). Each process is curved on the outer edge, and pointed antero-laterally, where it projects slightly beyond the posterior end of the transverse process of the more anterior vertebra (Text-fig. 13*b*). On the upper surface of the process is a slight crest, passing from the anapophysis to the antero-lateral point; it is best developed on *L.* 2 and *L.* 3, but is weaker on the more posterior lumbar vertebrae, on which the anapophysis is also reduced.

Below each transverse process of the lumbar and posterior thoracic vertebrae, and separated from it by a groove, is the lateral keel of the ventral surface of the centrum. This is absent in *Echinosorex*, in which the transverse processes are placed lower down on the vertebrae, and it is extremely faint in Recent Erinaceinae, but it occurs in *Hylomys*. The ventral surfaces of the lumbar vertebrae are marked by concavities for the psoas muscles, separated by a median crest which is not so strongly developed as in *Echinosorex*, but is lacking in Recent Erinaceinae. Intercentra are present in the lumbar region, as transverse pieces of bone wedged between the centra; the most anterior is placed between *Th*. 12 and *Th*. 13, the most posterior between *L*. 5 and *L*. 6. According to Leche (1902) these occur in *Erinaceus* and *Hylomys*, but in *Echinosorex* they are present only in the tail.

Three sacral vertebrae are preserved (Text-fig. 13*a*, 13*c*). The neural spines of *S*. 1 and *S*. 2 are rectangular in side view and nearly touch each other as in *Echinosorex*; in Recent Erinaceinae they are more triangular and widely separated. The spine of *S*. 3 is broken. The metapophysis of *S*. 1 is fairly well developed, though smaller than those of the lumbar region; the metapophysis of *S*. 2 is much smaller. The sacral metapophyses are closer to the neural spines than in the lumbar vertebrae, but are not closely applied to them as in *Echinosorex*. The space on the upper surface of the sacrum for the sacrococcygeal muscles is therefore less enlarged than in *Echinosorex*. and more like *Erinaceus*; this would seem to indicate that the tail was not greatly enlarged. The ventral surface of the sacrum is more convex than in Recent Erinaceinae, and resembles *Echinosorex*. What appears to be an intercentrum is fused to the sacrum between *S*. 2 and *S*. 3. No vertebrae are preserved beyond the broken *S*. 3.

RIBS AND STERNUM.—The thorax is badly crushed laterally, and it is not possible to determine with certainty whether it was narrow as in *Echinosorex* or broad as in *Erinaceus*. The relatively low insertion of the ribs on the thoracic vertebrae suggests a resemblance to *Echinosorex*; the longest ribs are, however, longer in proportion to the length of the thoracic vertebrae than they are in *Echinosorex* but not so long as in *Erinaceus*.

In cross-section the ribs of *Erinaceus* are flattened transversely, so that the area of attachment of the intercostal muscles is relatively small. In *Echinosorex* the cross-section is much broader than long, and the muscle crest on the posterior outer border is strongly developed. The ribs of *Gymnurechinus* are intermediate in shape: the cross-section approximates to an equilateral triangle.

The manubrium sterni (Text-fig. 12*j*) closely resembles that of *Echinosorex*, and differs markedly from the shorter, flattened structure found in Recent Erinaceinae. It approaches *Erinaceus*, however, in the more transverse anterior border. Near it is a structure which appears to be the calcified broadened lower end of the first rib. Lying across the posterior end of the manubrium is an elongated, flat, symmetrical bone which has some resemblance to the xiphisternum of *Echinosorex*, but no other sternalia seem to be preserved.

PECTORAL GIRDLE AND FORE-LIMB.—A fragment of the clavicle shows this to have been a slender bone, somewhat more curved than in *Echinosorex* or *Erinaceus*. The scapula is badly preserved, but appears to have a well-developed metacromion process as in Recent Erinaceidae.

The greater part of the left humerus is preserved in Rs 424.48, but the upper part is missing. Three other humeri have been found at the same site (Rs 424c.48), all of which lack the lower end and the upper epiphysis.

The humerus agrees very closely in shape with those of *Echinosorex gymnurus* and

Erinaceus europaeus. Its length is estimated as 33.5 mm. (allowing 3·5 mm. for the unknown upper epiphysis); its width at the lower end is 8·8 mm., and its width at the narrowest part of the shaft is 3 mm. The upper surface of the shaft, where it articulates with the epiphysis, is well preserved in one of the specimens in Rs 424c.48. It is roughly rectangular in outline, its longer axis running from antero-lateral to postero-medial, and it is divided by two low ridges at right angles into four basins, anterior, medial, posterior and lateral in position, corresponding to the corners of the rectangle. The ridge separating the anterior and lateral basins is rather faint. Where the ridges meet the surface of the humerus, the epiphysial line rises: just posterior to the bicipital groove, between the head and the lesser tuberosity, between the greater and lesser tuberosities, and below the greater tuberosity on the antero-lateral side of the bone. At intermediate positions the basins fall away towards the surface of the bone, especially the posterior basin (below the head), and the epiphysial line accordingly falls at four places. In *Echinosorex* the epiphysial line is exactly similar, but certain differences were noticed in *Erinaceus.* In that genus the epiphysial surface has rather the shape of a parallelogram with the transverse diameter longer than the anteroposterior diameter. The ridges on the surface are less clearly indicated; there is no ridge separating the anterior and lateral basins; and the epiphysial line on the anterior part of the humerus is nearly horizontal. The upper part of the humerus by the deltoid crest is more flattened antero-posteriorly in *Erinaceus.*

The muscle crests on the shaft are closely similar in the three species examined: there is a moderately developed deltoid crest, which arises below the posterior part of the greater tuberosity and passes forward to reach the anterior border of the humerus about half-way down the shaft; on the anterior border a rounded ridge represents the insertion of the pectoral muscle and fades out about two-thirds of the way down the shaft. The shallow bicipital groove is posterior to the top of this ridge. About one-third of the way down the shaft, near the posterior margin of the medial surface, is a short crest for the m. latissimus dorsi. The posterior part of the shaft near its lower end is flattened for the third head of the triceps. Two specimens in Rs 424c.48 display a posterolateral nutrient foramen a little below the middle of the shaft; a similar foramen occurs in *Echinosorex* and in most specimens of *Erinaceus europaeus.* A medial foramen a little further down the shaft, which occurs fairly constantly in *Erinaceus,* could not be detected in *Gymnurechinus* or *Echinosorex.*

The lower end of the humerus is fully preserved in Rs 424.48 (Text-fig. 13*f*). It closely resembles those of *Echinosorex, Amphechinus arvernensis* (Lavocat 1951), and *A. intermedius* (Gaillard 1899) but in the last species the humerus is thicker at the upper end. An entepicondylar foramen is present. The entocondyle is larger than in Recent Erinaceinae, and has the same shape as in *A. arvernensis.* On its posterior surface is a depression, present also in *Amphechinus* and *Erinaceus,* but absent in *Echinosorex,* for the medial ligament of the elbow joint. The olecranon fossa is perforated at its greatest depth by the epitrochlear fenestra, which resembles that of *Echinosorex* in being smaller than in *Erinaceus* and confined to the lateral side of the fossa. The ectocondyle is not so well developed as in *Erinaceus europaeus,* but resembles those of *Echinosorex, Amphechinus, Hemiechinus auritus* and *Erinaceus algirus.* Immediately above the medial trochlear keel, on the posterior side of the humerus, is a small foramen which may be seen in Recent Erinaceidae.

The humerus of *Gymnurechinus* also resembles a specimen referred to *Peratherium* by Schlosser (1887, pl. 3, fig. 38), which may belong to *Neurogymnurus*. The humerus of *Galerix exilis* (Fraas 1870; Schlosser 1887) differs in the greater size of the epitrochlear foramen. A specimen figured by Gervais (1859, pl. 44, fig. 21) as *Cricetodon* sp., but compared with *Galerix* by Fraas (1870), is very much like *Gymnurechinus*: it resembles *Gymnurechinus* and differs from *Galerix* in the small size of the epitrochlear fenestra, but the entepicondyle is weaker than in *Gymnurechinus*. In *Mioechinus sansaniensis* (Depéret 1887) there is no entepicondylar foramen.

A small part of the ulna is preserved, showing the vicinity of the elbow-joint, but displaying no distinctive characters.

PELVIS AND HIND-LIMB.—In the pelvis (Text-fig. 13*g*, 13*h*, 13*i*), the tip of the ilium and most of the post-acetabular region are missing. The spina posterior ilii is situated farther forward in relation to the acetabulum than in Recent Erinaceidae: the distance from the anterior edge of the acetabulum to this spine is about two and a half times the diameter of the acetabulum, whereas in all Recent Erinaceidae it is about one and a half times. The upper surface of the ilium is flatter than in *Echinosorex* and Recent Erinaceinae, but in this respect seems to resemble *Galerix* (figured by Fraas 1870, and Leche 1883), and *Amphechinus* (Lavocat 1951). Also as in *Galerix* and *Amphechinus*, the lateral edge of the ilium forms a sharp crest in front of the tuberosity for the origin of m. rectus femoris, whereas in Recent Erinaceidae it is more rounded. A shallow depression for m. glutaeus minimus occurs antero-dorsally to the acetabulum; it is bounded medially by a low ridge which runs parallel to the medial border of the ilium and probably demarcates the origin of m. glutaeus maximus, as in *Echinosorex*. The cotyloid notch is narrower than in Recent Erinaceinae but not so narrow as in *Echinosorex*; it forms about one-eighth of the circumference of the acetabulum. The spine of the ischium appears to have been moderately developed; its exact shape is unknown.

The lower edge of the innominate bone, antero-ventral to the acetabulum, is developed into an internally directed flange, as in *Echinosorex* and probably also in *Galerix*, and terminates in a tubercle for m. pectineus. The flange is much weaker in Recent Erinaceinae. On the edge of the flange, anterior to the tubercle for m. pectineus, is a small process for m. psoas minor, which also occurs in *Erinaceus* (Leche 1883). The internal surface of the innominate, above the flange, is deeply concave as in *Echinosorex*; in *Erinaceus* the concavity is much less. The more posterior and ventral part of the concavity probably served for attachment of m. obturator internus. In *Echinosorex* the upper edge of the concavity is developed into a distinct crest for the origin of m. iliococcygeus, but this crest is very faint in *Gymnurechinus*, as in *Erinaceus*; the tail of *Gymnurechinus* was, therefore, probably small.

The small part of the pubis that remains in the fossil indicates a backward rotation, as in *Galerix*, *Amphechinus* and Recent Erinaceidae, and the pubic symphysis was probably reduced.

The femur (Text-fig. 13*d*) lacks the extreme lower end; as preserved, the bone is 34 mm. long. The head has been slightly misplaced, but in its natural position it was less in line with the shaft than in *Erinaceus*, thus resembling *Echinosorex* and *Amphechinus* (Lavocat 1951). On the head is a pit for attachment of the ligamentum teres, as in *Echinosorex*. This ligament is stated by Leche (1883) to be absent in the Recent Erinaceinae: the pit for its attachment is absent in *Erinaceus europaeus* and *Hemiechinus auritus*, but it occurs in a specimen of *Erinaceus algirus*. The greater and lesser trochanters of *Gymnurechinus* are similar to those of Recent Erinaceidae; they are joined on the posterior side by a trochanteric crest, which defines a deep fossa for the m. obturator externus. In *Erinaceus* the trochanteric

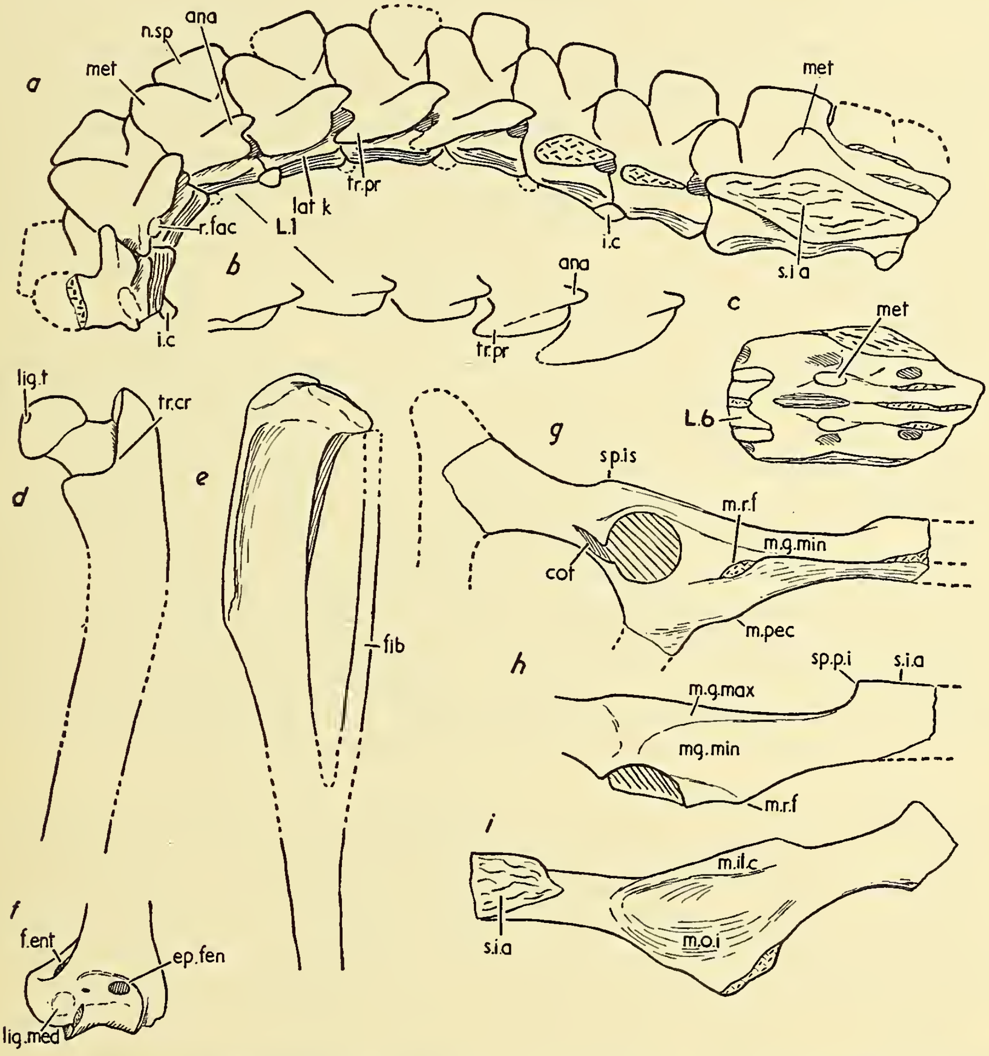


FIG. 13. *Gymnurechinus camptolophus*, Rs 424.48. ×2. (*a*) Th. 13–S. 3, side view. (*b*) Transverse processes of Th. 14–L. 4, dorsal view. (*c*) Sacrum, dorsal view. (*d*) Right femur, posterior view. (*e*) Left tibia and fibula, lateral view. (*f*) Lower end of right humerus, posterior view. (*g*), (*h*) and (*i*) Right pelvis, lateral, dorsal and medial views.

ana, anapophysis; *cot*, cotyloid notch; *ep.fem*, epitrochlear fenestra; *f.ent*, entepicondylar foramen; *fib*, fibula; *i.c*, intercentrum; *L* 1, *L* 6, first and last lumbar vertebrae; *lat.k*, lateral keel; *lig.med*, origin of medial ligament of elbow; *lig.t*, insertion of ligamentum teres; *met*, metapophysis; *m.g.max*, origin of glutaeus maximus; *m.g.min*, origin of glutaeus minimus; *m.il.c*, origin of iliococcygeus; *m.o.i*, origin of obturator internus; *m.pec*, origin of pectineus; *m.r.f*, origin of rectus femoris; *n.sp*, neural spine; *r.fac*, facet for last rib; *s.i.a*, sacro-iliac articulation; *sp.is*, spina ischii; *sp.p.i*, spina posterior ilii; *tr.cr*, trochanteric crest; *tr.pr*, transverse process.

crest is much weaker, but *Echinosorex* and *Amphechinus* closely resemble *Gymnurechinus*. A crest for the insertion of m. glutaeus maximus represents the third trochanter, and passes down the lateral side of the shaft as in other Erinaceidae.

The tibia (Text-fig. 13*e*) is also incomplete at its lower end. The articular surface does not differ from that of Recent Erinaceidae. The anterior crest, for the origin of m. tibialis anticus, is more strongly developed than in *Erinaceus*, but agrees with *Echinosorex*. The fibula is united distally with the tibia as in other Erinaceidae.

Lying near and roughly parallel to the clavicle, and crossing the long axis of the manubrium sterni approximately at right angles, is a metatarsal which may be referred provisionally to the same individual. Its proximal end is slightly damaged, and the distal epiphysis is missing. The bone is 17 mm. long and 3·3 mm. wide at its distal end. Unless the feet were very abnormal, it is much too long to be a metacarpal. Approximately in line with it is a broken basal phalanx closely resembling those of *Echinosorex*. It is 7 mm. long, and a little shorter in proportion to the metatarsal than in the middle toes of *Erinaceus* and *Echinosorex*.

PROPORTIONS OF THE BODY (Table 12; Text-fig. 14).—The head was larger in proportion to the body than in *Echinosorex* and Recent Erinaceinae, but not as large as in *Hylomys*. The neck is longer in proportion to the trunk than in Recent Echinosoricinae, and in these it is again longer than in the Recent Erinaceinae. The length of the thorax, in proportion to the length of the lumbar region, measured between the head of the last rib and the acetabulum, is not so great as in *Echinosorex*, but greater than in *Hylomys*; in the Recent Erinaceinae the thorax is relatively much shorter. The ribs seem to be proportionately longest in *Erinaceus*, shortest in *Echinosorex*, and intermediate in *Gymnurechinus*. Judging by the origins of the mm. sacrococcygeus and iliococcygeus, the tail was probably small in *Gymnurechinus*, perhaps like that of *Hylomys*. The remains of the femur, tibia and humerus indicate that the limbs were at least as long in proportion to the body as in *Erinaceus*; if the metatarsal is correctly identified, the feet were longer than in *Erinaceus*.

RELATIONSHIPS OF *GYMNURECHINUS CAMPTOLOPHUS*.—The skull of this species shows such a close resemblance to that of *G. leakeyi* that there can be no doubt that the two species are very closely allied. Most of the differences, perhaps hardly more than of subspecific value, indicate that *G. camptolophus* is somewhat more advanced. The greater prominence and broader dorsal development of the condyles, with corresponding differences in the atlas, show a higher degree of specialization of the neck. The sharper sagittal crest and the median extension of the ridges on the parietal indicate a stronger development of the temporal muscle. The less transverse upper molars show an approach towards *Erinaceus*. The increased size also suggests an advance. The small hypocone of P^4 is probably an advanced, and not a primitive character, as this cusp is almost universally developed in Erinaceidae. It may be concluded, therefore, that *G. camptolophus* is a derivative of *G. leakeyi* and thus probably a little later in time.

The almost completely echinosoricine skeleton confirms the view that *Gymnurechinus* is a very primitive member of the Erinaceidae. Among the numerous resemblances to *Echinosorex* already noted may be recalled the enlarged neural spines and the hypapophysial spines of the axis and other cervical vertebrae, the enlarged

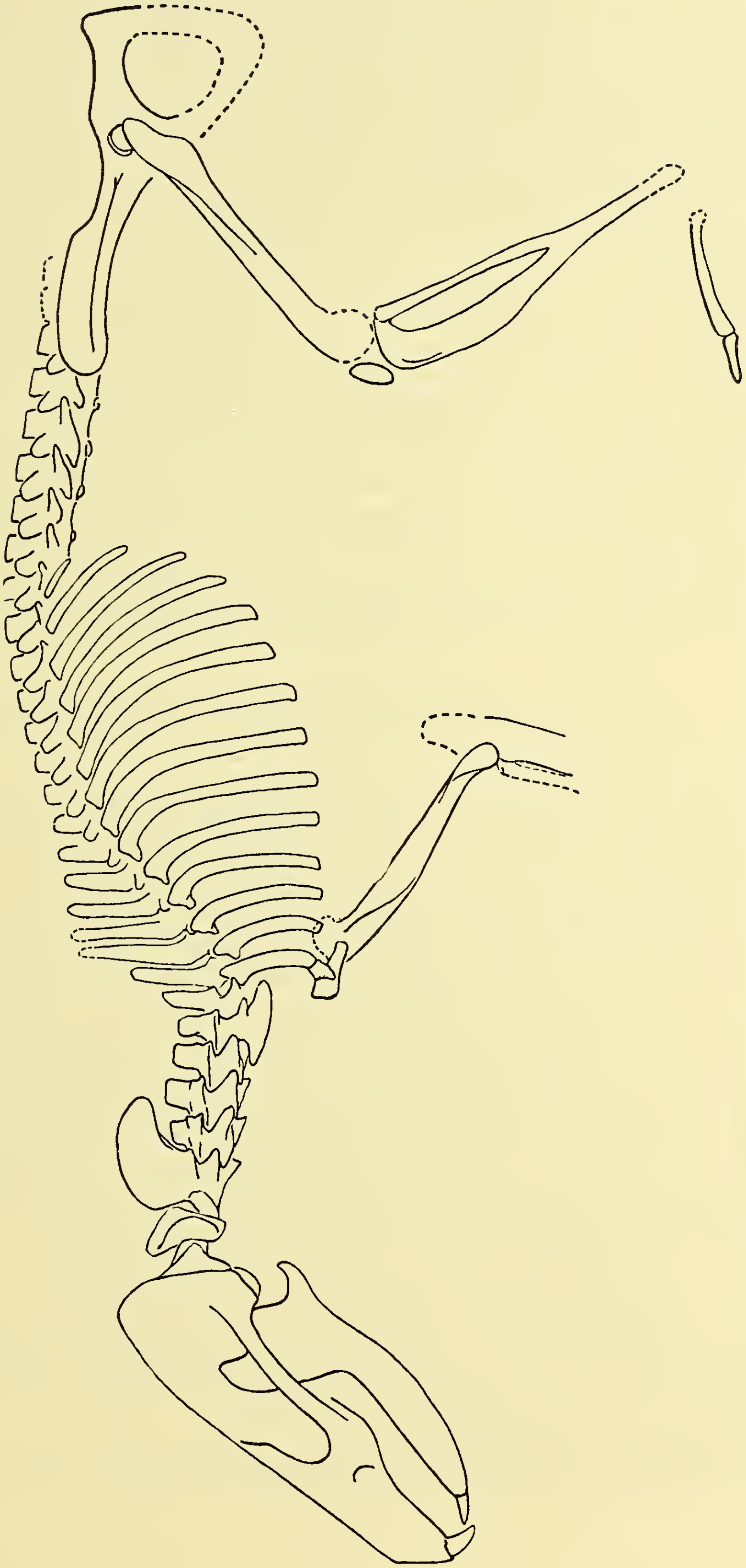


Fig. 14. *Gymnurechinus camptolophus*, Rs 424.48. Reconstruction of skeleton. Natural size.

neural spines of the anterior thoracic vertebrae, the rectangular neural spines of the lumbar and sacral vertebrae, the characters of the manubrium, the entepicondylar foramen, the small epitrochlear fenestra of the humerus, the deep internal concavity of the pelvis, the presence of a ligamentum teres, the strong development of the anterior crest of the tibia, the long neck, and the relatively short lumbar region. Echinosoricine characters also predominate in *Amphechinus*, to judge from those parts of the post-cranial skeleton that are known (Lavocat 1951). The entepicondylar foramen and the ligamentum teres occur as primitive survivals in some Recent members of the Erinaceinae.

In some other respects, where *Gymnurechinus* differs from *Echinosorex* it resembles *Hylomys*: the diaphragmatic vertebra is *Th.* 11; the transverse processes and other features of the lumbar vertebrae are very similar; intercentra are present in the lumbar region; the head is relatively larger than in *Echinosorex*, and the tail is probably shorter. The pelvis shows a close resemblance to that of *Galerix*.

Special resemblances to Recent Erinaceinae are few: atlas without hypapophysial spine; rudimentary pleurapophysis on *C.* 3 (*Hemiechinus*); ribs relatively longer than in *Echinosorex*, but not so long as in Recent Erinaceinae; diaphragmatic vertebra *Th.* 11 (*Hemiechinus*); intercentra in lumbar region; pit on humerus for internal lateral ligament of the elbow-joint; short tail. Some of these characters are shared with *Hylomys*, and may be primitive characters lost in *Echinosorex* (lumbar intercentra) or parallel developments in *Hylomys* and the Erinaceinae (reduction of the tail).

Gymnurechinus is specialized in the high development of the neck and the anterior dorsal spines. The functional significance of this is discussed below.

SPECIALIZATIONS OF THE SKELETON OF *ERINACEUS*.—At the present day, the Erinaceinae differ strikingly from the Echinosoricinae in their skin. Not only have the hairs over the back been converted into spines, but there has been a great development of the skin musculature. In a hedgehog (*E. europaeus*) weighing 529 gm., the skin with its muscles weighed 180 gm., or 34% of the body weight. In most mammals the skin makes up 13 to 20% of the body weight: examples of comparable size are a rabbit weighing 662 gm. (18%), a squirrel (*Sciurus carolinensis*) weighing 323 gm. (14%), and a rat (*Rattus norvegicus*) weighing 354 gm. (16%); in a cat weighing 2216 gm. the skin was 12% of the body weight. The skin musculature also shows an anatomical structure different from that of the Echinosoricinae (Dobson 1882, Leche 1902): its main constituent is the m. orbicularis panniculi, a broad band which extends along the sides as far as the edge of the spine-covered area, and passes over the neck and sacrum to form a sphincter enclosing the body. This muscle must considerably impede movements of the vertebral column, especially dorsal flexion, and one would expect the vertebral musculature to be weakly developed. Slijper (1946) regards *Erinaceus* as more primitive than *Echinosorex* in the weaker differentiation of the transversospinalis musculature in the pre-lumbar region. It seems better, however, to regard this character as a secondary consequence of loss of mobility of the back: according to Slijper it is shared with *Dasypus* and the Chiroptera, which also have poor mobility of the back.

The comparative weights of a number of groups of muscles in *Erinaceus europaeus*, a rat, a squirrel and a cat are given in Table 13. It will be seen that the development of the skeletal musculature is much less in *Erinaceus* than in the other mammals. The muscles of the posterior part of the body are more reduced than those of the forelimb, shoulder and neck, but the total of these three groups is only 5·2% of the total weight, as compared with 8·7% in the rat, 8·9% in the squirrel, and 12% in the cat.

The weak musculature is reflected in the skeleton by the poor development of processes for muscle attachment. If *Erinaceus* is compared with *Echinosorex* this is apparent in the transverse processes of the atlas, the neural spines of the whole vertebral column, the hypapophysial spines of the cervical vertebrae, the transverse processes of the lumbar vertebrae, the keel on the manubrium sterni and the anterior crest of the tibia.

The skin musculature not only impedes the body movements, but also takes over some of the functions of the skeletal musculature. This is shown particularly in the mechanism of rolling up, in which the orbicularis panniculi, contracting like a sphincter, flexes the back in the lumbar region. The sphincter slips forward over the back of the head, pulled forward by the m. fronto-cuticularis, and so assists in the flexion of the head on the neck. It also slips back over the rump and pulls in the tail and the hind limbs. The short neck and the elongate lumbar region seem to be adaptations to this mechanism. The short, broad thorax, the short tail, the flattened posterior part of the skull, and perhaps the shortened snout, also increase the efficiency of the process by which the whole body becomes enclosed in the spine-covered dorsal skin.

The predominance of echinosoricine characters in the skeleton of *Gymnurechinus* shows that it had not acquired the specializations characteristic of the Recent Erinaceinae. If the foregoing argument is sound, the animal was probably hairy rather than spiny on its dorsal surface, like *Echinosorex* and *Hylomys*.

SPECIALIZATIONS OF *GYMNURECHINUS CAMPTOLOPHUS* AND *G. LEAKEYI*.—A number of features of the skull and skeleton, namely, the development of the neck and the posterior part of the skull, the length of the dorsal spines, and the roughness of the surface of the skull remain to be explained.

The muscles of the neck may be reconstructed as follows:

TRANSVERSO-SPINALIS.—Originated by a number of slips from the metapophyses of the anterior thoracic vertebrae and from the lower part of the neural arches of *C*. 3–7, to pass forwards and upwards and insert to the upper part of the neural arches and neural spines of the cervical vertebrae, including a more extensive insertion into the spine of the axis near its posterior border: a dorsal flexor of the neck. The origins and insertions of this muscle are more clearly indicated by grooves and prominences of the cervical vertebrae than in *Echinosorex*, and the muscle was probably better developed.

OBLIQUUS CAPITIS INFERIOR.—Originated from the lateral surface of the spine of the axis; inserted into the upper and posterior surface of the transverse process of the atlas. Rotated the atlas on the axis; the muscles of both sides acting together extended the axis-atlas joint. The origin and insertion of this muscle are much more extensive than in *Erinaceus*, and somewhat more so than in *Echinosorex*.

RECTUS CAPITIS POSTICUS MINOR.—Originated from the neural arch of the atlas;

inserted broadly into the occipital surface of the skull on either side of the median crest. The two muscles acting together extended the joint between the skull and the atlas. The greater height of the occiput as compared with *Erinaceus* increased the leverage of this muscle. Its area of insertion is more concave and more roughened than in *Erinaceus*, and the muscle was probably more powerful.

RECTUS CAPITIS POSTICUS MAJOR.—Originated from the anterior edge of the spine of the axis; inserted into the occiput, laterally to the m. rectus capitis posticus minor. It was a longer and more slender muscle than the m. rect. capit. post. minor, which it assisted in extending the head on the neck.

OBLIQUUS CAPITIS SUPERIOR and RECTUS CAPITIS LATERALIS.—Originated close together on the anterior surface of the transverse process of the atlas. The m. obl. capit. superior passed forwards and upwards, to insert behind the posterior lambdoid crest; the m. rectus capit. lateralis inserted below it, on the medial face of the paroccipital process. The m. obl. capit. superior assisted in extension of the occipital joint, and both muscles caused abduction. The m. obl. capit. superior, at least, was better developed than in Recent Erinaceidae.

SEMISPINALIS CAPITIS.—Originated from the lateral crest of the cervical vertebrae, near the posterior zygapophyses; inserted probably as in *Erinaceus* under the occipital crest, above the m. rect. capit. post. minor. Extensor of the head. The greater height of the occipital surface of the skull of *Gymnurechinus* would increase the leverage of this muscle.

TRAPEZIUS, CLEIDO-OCCIPITALIS and RHOMBOIDEUS ANTICUS.—Originated from the scapula and clavicle as thin sheets of muscle which inserted into the nuchal and anterior lambdoid crests. Played a minor part in extension and abduction of the head and neck. The height of the occipital crest may indicate that they were better developed than in *Erinaceus*.

SPLENIUS.—Originated from the elongated anterior thoracic neural spines; inserted behind the anterior lambdoid crest. This muscle, which must have been strongly developed in *Gymnurechinus*, seems to function mainly as an abductor. In *Erinaceus* its insertion extends higher up on the skull, above the posterior lambdoid crest on to the occipital crest. According to Evans (1939) it extends almost to the occiput in *Didelphis* and *Felis*, and at least the upper part of it functions as an extensor of the head. It is possible that in *Gymnurechinus* it had divided into a dorsal extensor part, inserted in the occipital crest, and an abductor part, inserted in the anterior lambdoid crest.

LONGISSIMUS GROUP.—Just below the pit for the insertion of the splenius is another, which must have provided insertion for the trachelo-mastoideus (longissimus capitis). Other parts of the longissimus muscle inserted into the transverse processes of the atlas and other cervicals. They originated from the lateral crests of the more posterior cervicals, near the anterior zygapophyses. These muscles were abductors, and probably also flexors, of the head and neck.

STERNO-MASTOIDEUS.—Originated in the manubrium sterni; inserted into the mastoid process below the trachelo-mastoid. Flexor of the head. Probably stronger than in *Erinaceus*.

RECTUS CAPITIS ANTICUS MAJOR ET MINOR.—Originated in the ventral arch of the atlas near the base of the transverse process (r.c.a. minor), and on the pleurapophyses of the cervical vertebrae up to *C*. 6. Inserted to the ventral surface of the basioccipital: the m. rect. capit. antic. major between the posterior parts of the bullae, near the basisphenoid suture, and the m. rect. capit. antic. minor behind it in an oblique area extending towards the jugular foramen. They formed part of the longus colli system, of which other slips were inserted into the sides of the hypapophysial spines of the axis and other cervical vertebrae. Flexors of the head and neck. The cervical part (longus colli) was more strongly developed than in *Erinaceus*. The leverage of the cranial part of the system was increased by the greater length of the basioccipital bone.

From this analysis one may conclude that the neck of *Gymnurechinus camptolophus*, and presumably also that of *G. leakeyi*, was capable of more powerful movements in all directions than that of *Erinaceus*, and that it somewhat exceeded *Echinosorex* in this respect.

Slijper (1946) ascribed the elongation of the neural spines of the anterior thoracic vertebrae of many mammals to the necessity to provide attachment for the splenius, spinalis cervicis and ligamentum nuchae, which support the head, but failed to find any close correlation between the height of the spines and the size of the head or the length of the neck. The ligamentum nuchae is well developed only in ungulates and Carnivora, but traces of it have been found in other mammals, notably *Erinaceus* (Slijper 1946). It is possible that in *Gymnurechinus* the median dorsal septum of the neck was somewhat fibrous and played a part in supporting the relatively large head. The spinalis cervicis is not differentiated from the transverso-spinalis musculature in Recent Erinaceidae. That the splenius of *Gymnurechinus* was well developed, was probably the main cause of the elongation of the spines. However, at least part, and possibly the whole, of the splenius was inserted too low down on the side of the skull to have supported the head efficiently. It seems more likely that the main function of the splenius in *Gymnurechinus* was to move the head, and that mobility of the head, rather than its size alone, must be taken into account as a factor determining the length of the dorsal spines of other mammals.

Long neural spines occur on the anterior thoracic vertebrae of Carnivora (*Felis*, *Hyaena*, *Canis*) and *Thylacinus*, which have a mobile neck used in feeding; of *Sus*, which digs with its snout; of the Bovidae, and of *Equus*, which not only show considerable mobility of the head on the neck while grazing, but can raise their heads rapidly when alarmed. They are also present in *Lepus*, *Dasyprocta* and other rodents, perhaps again correlated with raising the head, and in *Elephas*, which not only has to support a heavy head but also has to move it when using its tusks. On the other hand, the dorsal spines are very short in a number of forms in which the neck is less mobile: *Myrmecophaga*, *Manis*, the sloths, *Talpa*, *Sorex*, the bats, *Phascolarctos*, the lemurs, and the squirrels; the last two groups raise the whole body, rather than the head only, when alarmed, and when feeding replace the mobility of the head by that of the fore-limbs.

The structure of the surface of the bone in the temporal region of the skull remains to be considered. An analogous structure commonly occurs in dog skulls, where ridges on the surface of the bone cover the area of origin of the temporalis muscle. They are less prominent than in *Gymnurechinus*, and closer together in proportion to the size of the skull. As in *Gymnurechinus* they anastomose frequently, but are not so regular in their arrangement, although they show the same tendency to run from antero-dorsal to postero-ventral. A similar feature was noticed in skulls of *Putorius*, *Mellivora*, *Nasua*, *Thylacinus* and *Dasypus*, and rather fainter sculpturing is fairly widespread in mammals, apparently occurring more frequently among those with powerful jaw muscles. The exaggeration of this character in *Gymnurechinus* might be due to a somewhat more tendinous origin of the m. temporalis than in other mammals. Such a muscle, with relatively short fibres, would be particularly adapted for gripping rather than for normal chewing movements. The anterior teeth, including the paraconid of P_4, would also seem to be effective in gripping.

Only in *Erinaceus*, of the existing Erinaceidae, has the behaviour been described at all fully (Herter 1938). This form feeds mainly on invertebrates of relatively large size, such as carabid beetles, cockroaches and earthworms, and the other members of the family, including the Echinosoricinae, seem to have a similar diet. *Erinaceus* is also recorded as feeding on fruit, and it readily kills and eats amphibians, reptiles and small mammals. It seeks its food by grubbing in dead leaves, loose soil and similar situations, using the snout, aided by the fore-feet, and depending almost entirely on the sense of smell. If its prey escapes the hedgehog does not chase it, and in this respect differs strikingly from a true carnivore. *Echinosorex* has been observed to catch small fish in shallow water (Harrison 1950).

Gymnurechinus seems to have been a somewhat more active animal than *Erinaceus*, though its vertebral column shows it to have been an ambulatory form without any leaping-cursorial adaptations. The large size of the petrosal lobe of the paraflocculus is a characteristic of relatively active mammals (cf. Olson 1944). The smaller size of the olfactory chamber is accompanied by a somewhat greater development of that part of the cerebral cortex corresponding to Brodmann's (1909) area 17, which is concerned with the sense of sight. A slightly greater dependence on sight and less on smell would be expected in a more rapidly moving animal, but it is unlikely that *Gymnurechinus* differed very much from *Echinosorex* in this respect.

The principal adaptive specialization of *Gymnurechinus* seems to have been for gripping objects with the teeth and pulling with the powerful neck-muscles. A somewhat similar action is performed by *Erinaceus* when feeding on a carcass, and it is possible that *Gymnurechinus* was, to some extent, a carrion-feeder. Alternatively, it is possible that the tearing action was not used in feeding, but in the search for food. If its food consisted largely of insects and other invertebrates, it would find a rich source of supply of these under loose bark of dead trees or between the leaf-sheaths of monocotyledonous plants. I am informed by Dr. W. D. Hincks that entomologists collecting in tropical forest obtain a large proportion of their specimens from such situations. One may therefore imagine *Gymnurechinus camptolophus* gripping pieces of loose bark or leaf-sheaths with its teeth and tearing them off to obtain its food.

Gymnurechinus songhorensis sp. nov.

(Plate 3, figs. 18, 19, 24–26, Pl. 4, fig. 34; Text-figs. 8*c*, 9*c*, *f*, 15)

DIAGNOSIS.—Differing from other species of the genus in the less elevated occiput, the small lambdoid area, the weak posterior lambdoid crest, the smaller paroccipital processes, and the weaker dorsal development of the condyles. Sagittal crest sharp; M^1 as long as broad; hypocone of P^4 well developed. Width of palate across paracones of first molars 18·7 mm., alveolar length of M_1–M_3 11·3 mm.

HOLOTYPE.—Sgr 513.49, the posterior part of a skull, from Songhor.

REFERRED MATERIAL.—This was the only species of *Gymnurechinus* found at Songhor, where the following specimens were obtained:

Sgr 62.47. A skull with lower jaw.

Sgr 452.48. A maxillary fragment with unworn P^3–M^1 and the anterior border of the orbit.

Sgr 79.48. A fragment of a juvenile lower jaw containing unerupted M_3.

The only specimen from Rusinga definitely identified as this species is Rs 32a.32, a cranium, of uncertain provenance. It corresponds closely with the holotype. The fragments of mandible Rs 145.41 and Rs 732.47, referred to *G. camptolophus*, might belong to the present species.

That this species appears to replace *G. leakeyi* at Songhor, indicates a difference either of geological age or of facies. All the specimens of *G. songhorensis* are reddish brown, whereas those of *G. leakeyi* are whitish or tawny; this again suggests a difference of facies.

THE SKULL.—The holotype cranium is slightly distorted by dorsoventral crushing; Rs 32a.32 is uncrushed, but somewhat weathered; Sgr 62.47 permits measurements of the facial region.

Measurements of the face are 10–15% larger in all dimensions than in *G. leakeyi*, and agree with those of *G. camptolophus*, but the posterior part of the skull is proportionately smaller, so that the skull as a whole is only 5% longer than in *G. leakeyi*. The cranium agrees in width with that of *G. leakeyi*, but is about 10% shorter in the postglenoid region. The occiput is 6% lower than in *G. leakeyi*. The disproportion between the face and the cranium is therefore greater than in *G. camptolophus* (Table 2; Text-fig. 8*c*).

The nasals extend back as far as in *G. leakeyi*, but are slightly narrowed near the middle of their length because of an overlap of the premaxillae. Other features of the face shown on Sgr 62.47 and Sgr 452.48 resemble *G. leakeyi*, except for the larger size. Little of the palate is visible, and it is not known whether it was perforated.

The most striking differences are to be found in the posterior part of the skull (Text-fig. 9*c*, 9*f*; Pl. 3). The sagittal crest is sharp and high, and divides posteriorly into two slightly divergent crests, separated by a deeply concave area at the occiput. The median crest on the supraoccipital is much weaker than in *G. leakeyi*. The anterior lambdoid crest is much stronger than the posterior one; it is joined by the crest which passes back from the upper edge of the root of the zygoma. As in *Erinaceus*, the scar for the splenius muscle extends above the top of the posterior lambdoid crest. The surface of the bone in the temporal region is rugose as in other members of the genus; the ridges extend over the parietal up to the sagittal crest as in *G. camptolophus*. The mastoid is exposed on the side of the skull, but not so extensively as in *G. leakeyi*.

The foramina of the orbito-temporal region resemble those of *G. leakeyi*. An alisphenoid canal is present. The auditory bulla is relatively shorter than in *G. leakeyi*, especially that part which is roofed by the alisphenoid. The bullae seem to be more widely separated than in *G. leakeyi* and *G. camptolophus*. The tympanic processes of the basisphenoid are less broad, and do not project so much below the base of the cranium, though this may be due to crushing. The recessus meatus is much smaller, and comparable in size with that of *Erinaceus*. The paroccipital process is comparatively weak. The crest which connects it to the mastoid process is deeply grooved for the hyomandibular nerve. The more medial crest which passes forward from the paroccipital process is less strongly developed than in *G. leakeyi* and is more like that of *Amphechinus edwardsi*. The median keel on the basioccipital is only faintly indicated.

The occipital condyles are incompletely preserved. The antero-ventral border of the condyle has a bay for the condylar foramen as in *G. leakeyi*. The dorsal part of the condyle is not expanded laterally, and appears to be more weakly developed than in *G. leakeyi*. The upper edge of the foramen magnum is not emarginate. The occipital surface above the foramen magnum is smooth, and the pit in the mastoid for m. obliquus capitis superior is shallow. The occipital view of the skull in general approaches that of Recent Erinaceinae.

Measurements of the skull indicate that the brain, although more elongate than in *Erinaceus* or *Neurogymnurus*, was less so than in *G. leakeyi* (Table 10).

The lower jaw of Sgr 62.47 agrees with *G. leakeyi* except for its greater size (Table 3).

DENTITION.—The worn teeth are visible in side view in Sgr 62.47, but show no visible differences from those of *G. camptolophus*. The diameter of I_2 at the base is 18% of the length of M_{1-3}. Sgr 452.48 shows P^3, P^4 and M^1 in crown view (Text-fig. 15; Pl. 4, fig. 34).

P^3 possesses a rudimentary hypocone. The hypocone of P^4 is well developed, and is slightly more lingual than the protocone: in *G. leakeyi* the two cusps are more nearly in line. M^1 is longer in proportion to P^4 than in *G. leakeyi*, and its buccal length is equal to its anterior width, as in *G. camptolophus* (Tables 4–6). The pattern

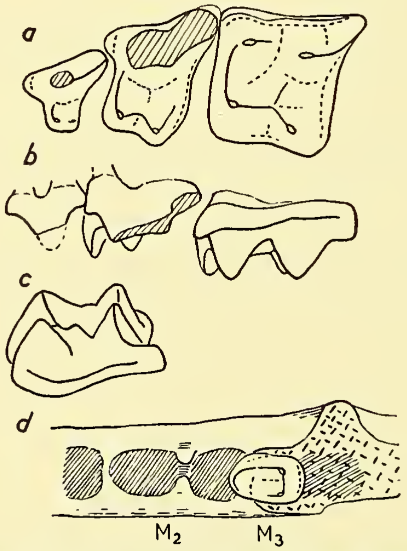


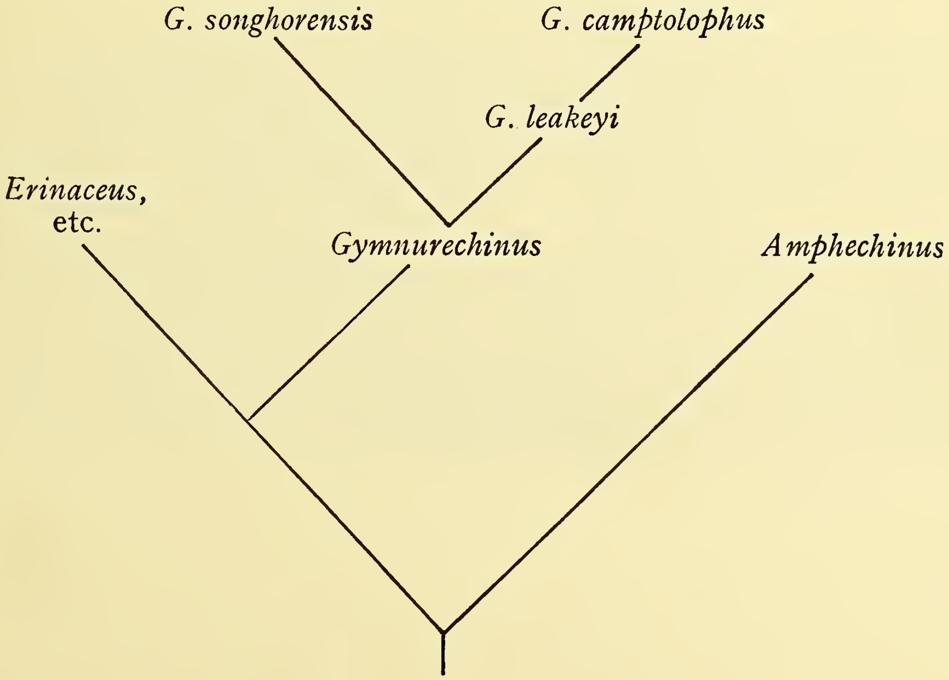
FIG. 15. *Gymnurechinus songhorensis*. (*a*), (*b*) P^3–M^1, crown and buccal views, Sgr 452.48. (*c*) M^1, posterior and slightly ventral view, Sgr 452.48. (*d*) Jaw fragment with unerupted M_3, crown view, Sgr 79.48. All ×4.

of M^1 resembles that of *G. leakeyi*, except for the difference in proportion. There is a small lingual cingulum between the protocone and hypocone. A small metaconule is present, though it is more reduced than in unworn specimens of *G. leakeyi* and *G. camptolophus*. The bottom of the groove between the paracone and metacone is slightly higher above the level of the buccal cingulum than in *G. leakeyi*.

Sgr 79.48 (Text-fig. 15*d*) consists of a fragment of mandible which seems to be referable to this species. The alveoli of M_2 are connected by a groove as in other Erinaceidae. The unerupted M_3 is embedded in the jaw near the base of the coronoid process. It closely resembles M_3 of *Erinaceus europaeus*, the talonid being represented only by a weak posterior cingulum. It is 2·4 mm. long and 1·8 mm. wide.

RELATIONSHIPS.—*Gymnurechinus songhorensis* resembles *G. leakeyi* in most respects, including the rugosity of the temporal region and the exposure of the mastoid above the anterior lambdoid crest. The two species are clearly related, but *G. songhorensis* differs from *G. leakeyi*, and resembles *G. camptolophus*, in the sharp sagittal crest, the dorsal extension of the ridges on the parietal, the larger face in proportion to the cranium, the less transverse M^1, and the slightly larger size. These features indicate that, like *G. camptolophus*, *G. songhorensis* represents a somewhat more advanced stage of evolution than *G. leakeyi*. At the same time it departs from both the other species of the genus in that P^4 is short in comparison with M^1, and in a number of characters of the posterior end of the skull: median occipital crest weaker; posterior lambdoid crest not continuous with occipital crest, but separated from it by the insertion of m. splenius; condyles less developed dorsally; paroccipital processes weaker; pit for m. obliquus capitis superior shallower; occipital surface less elevated; lambdoid triangle reduced; external auditory meatus small; tympanic chamber reduced. The characters of the occipital surface of the skull indicate a weaker development of the neck muscles: *G. songhorensis* has either avoided or lost this specialization of *G. leakeyi*, and so stands nearer to the Recent Erinaceinae. The smaller auditory meatus, as well as the proportions of P^4 and M^1, also approach *Erinaceus*. *G. songhorensis* thus provides additional evidence that *Erinaceus* has been derived from a member of the *Gymnurechinus* group.

The relationships of the species are expressed in the following diagram.



Genus *Amphechinus* Aymard, 1850.

Diagnosis.—Primitive Erinaceinae in which I^1 and I_2 are greatly enlarged; the root of I_2 terminates below P_4; the cheek teeth are displaced backwards in the skull so that P^4 stands partly under the orbit, and the molars are reduced in size.

Amphechinus rusingensis sp. nov.

(Pl. 4, figs. 28–31; Text-figs. 16, 17)

Diagnosis.—A species of *Amphechinus* that differs from *A. edwardsi* (Filhol) in the following characters: size smaller (C–M^3 inclusive 13·2–13·5 mm.); C and P^2_2 less reduced; P_2 with two roots; buccal edge of M^1 slightly longer than that of P^4; M_2 slightly larger in proportion to M_1 (length M_2/length M_1 0·82).

Holotype.—Rs 723.47, the facial part of a skull with associated mandible, from Hiwegi, sub-site R 1, Rusinga Island.

Referred Material.—From Rusinga: Rs 908.50, facial part of skull, from Hiwegi, sub-site R 1a; Rs 1398.50, fragment of mandible with P_4–M_2, from Kathwanga; Rs 553.48, fragment of mandible with P_4, from sub-site R 106.

From Songhor: Sgr 451.48, facial part of skull with P^2, P^3 and the lingual part of P^4; Sgr 319.49, fragment of mandible without teeth.

Proportions of the Skull (Table 15).—*Amphechinus rusingensis* is larger than *A. acridens* (Matthew & Granger) but smaller than *A. arvernensis* (de Blainville), *A. edwardsi* (Filhol) and *A. rectus* (Matthew & Granger). Measurements of the palate and teeth are 75–85% of corresponding measurements of *A. edwardsi*. The proportions of the skull are approximately the same as in that species, but the overall length of the maxillary dentition is proportionately a little greater. The holotype is crushed dorsally, and Rs 908.50 is crushed laterally; only in Sgr 451.48 can the interorbital part of the skull be seen in uncrushed condition. The last specimen shows that the mid-cranial part of the skull is lower in proportion to the width of the palate than in *A. edwardsi*, and it is probable that the skull as a whole was rather different in proportions in the two species.

Skull and Lower Jaw (Text-fig. 16; Pl. 4, figs. 28–30).—The nasals are parallel-sided and overlapped laterally by the premaxillae and maxillae; they extend above the orbits. Probably the premaxilla did not quite reach the frontal, but the crushed condition of the holotype, the only specimen in which the premaxilla is preserved, makes this uncertain. In front of the infraorbital foramen, the snout is formed equally of premaxilla and maxilla, as in *A. edwardsi*. The infraorbital foramen is above P^3, and P^4 is partly below the orbit. The zygoma arises opposite M^1; as seen in the holotype, it is more slender than in *Gymnurechinus*, and is less deeply hollowed out near its anterior end for the snout muscles. The groove above the anterior part of the orbit for the levator muscles also appears to be shallower than in *Gymnurechinus*, although crushing makes this difficult to determine with certainty. The jugal is present on the outer surface of the zygoma.

The postorbital processes and the frontal crests arising from them can be seen in the holotype and in Sgr 451.48. They seem to be much more weakly developed than in *Gymnurechinus*.

The palate is best preserved in Sgr 451.48 (Pl. 4, fig. 30), but it is also visible, though crushed, in Rs 908.50. It is extensively perforated. The vacuities, which almost meet in the middle line, are bounded laterally almost to the level of the anterior end of M¹, by a slender process of the palatine. On the maxillary portion of the palate, the longitudinal groove on either side of the mid-line is clearly visible. As far as can be seen, the palate extends posteriorly only a short distance behind the transverse crest.

Part of the inner wall of the orbit is visible in Sgr 451.48 and Rs 908.50. The lachrymal foramen opens into the orbit. The maxilla does not touch the alisphenoid. Optic and sub-optic foramina can be seen in the orbitosphenoid, and the naso-palatine foramen occurs at the confluence of the maxilla, orbitosphenoid and palatine. There is an ethmoid foramen in the lower part of the frontal, near the suture with the orbitosphenoid; another small foramen occurs in front of it, and a third opens higher up on the frontal, near the postorbital process. The orbital wall is very much like that of *A. edwardsi* (cf. Hürzeler, 1944, fig. 2).

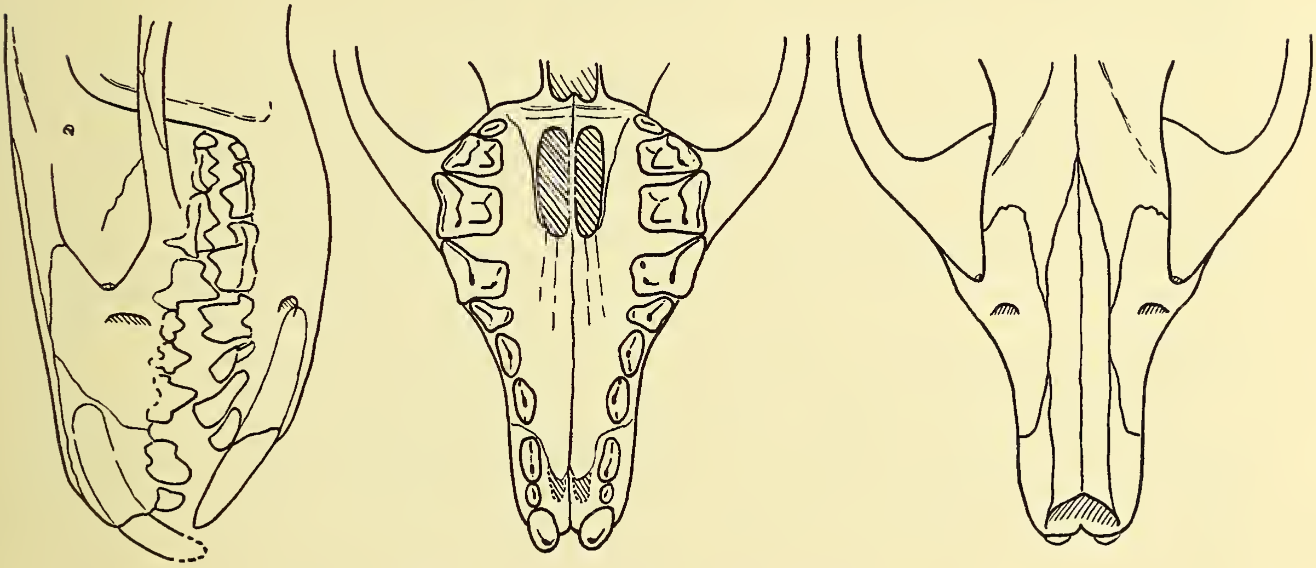


FIG. 16. *Amphechinus rusingensis*. Reconstruction of anterior part of skull, based on Rs 723.47, Rs 908.50 and Sgr 451.48. ×3.

In Sgr 451.48 part of the postorbital process has flaked away, revealing the cast of the space for the lateral concha of ectoturbinal N2 and the dorsal concha of ectoturbinal N3, very much as in *Gymnurechinus*. This specimen also shows a somewhat weathered cast of the anterior part of the dorsal side of the olfactory bulb. The relation of the olfactory chamber and the anterior end of the brain to the external features of the skull is the same as in *Gymnurechinus*.

The holotype shows the interior of the skull in the region of the optic foramina.

The optic nerves pass forward under a bridge of the presphenoid as in *Gymnurechinus* and *Erinaceus*. Shortly behind is the internal opening of the sphenorbital foramen, which leads into a groove in the floor of the brain-cavity corresponding to the cavum epiptericum, as in *Erinaceus*.

The lower jaw of the holotype has a more slender horizontal ramus than *A. edwardsi*, but the specimen is young, and in Rs 1398.50, Rs 553.48 and Sgr 319.49 the ramus is deeper. The posterior end of the jaw, with the condyle and angular process, is missing, but most of the coronoid process is present. The anterior edge of the coronoid process slopes back, as in other species of *Amphechinus* and in *Gymnurechinus*; it makes an angle of about 83° with the line of the teeth. The mental foramen is below the posterior part of P_4 in the holotype; in Rs 553.48 it is below the middle of P_4, and in Rs 1398.50 below the anterior part of P_4. The lower border of the mandible resembles that of *A. edwardsi*. The symphysis extends back to below P_2. A symphysial foramen is visible in Sgr 319.49.

UPPER TEETH.—The dental formula is $i.\frac{3}{2}$, $c.\frac{1}{1}$, $p.\frac{3}{2}$, $m.\frac{3}{3}$. The root of I^1 is preserved in the holotype. It is 1·8 mm. in antero-posterior diameter, and curves backwards above I^2 and I^3, to near the posterior edge of the premaxilla, causing a swelling on the outer surface of the bone. I^2 is a small, one-rooted tooth, resembling that of *A. edwardsi*. The diastema between I^1 and I^2 is 0·7 mm., i.e. relatively shorter than in *A. edwardsi*. I^3 is a larger tooth with two roots; its main cusp rises nearly vertically over the anterior end of the crown, and there is a lower but distinct posterior cusp. The diastema separating the canine from I^3 is shorter than in *A. edwardsi*.

The canine is a little higher and longer than I^3, and also has two roots. It has a laterally flattened main cusp, with anterior and posterior basal cusps; the anterior basal cusp is more distinct than in *A. edwardsi*. P^2 resembles the canine but is much smaller, though not so much reduced as in most specimens of *A. edwardsi*; it is as long as P^3, and resembles *A. arvernensis* in relative size. The main cusp has a sharp posterior crest, smaller anterior and posterior basal cusps, and a faint rounded cingulum; there are two roots.

The proportionate sizes of P^3–M^3 agree well with *A. edwardsi*, except that the buccal edge of M^1 is relatively longer: the buccal edge of M^1 is slightly longer than that of P^4, whereas in *A. edwardsi* it is slightly shorter (Tables 4–6; Text-fig. 17*a*).

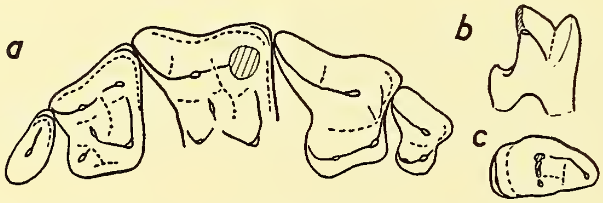


FIG. 17. *Amphechinus rusingensis*. (*a*) P^3–M^3, crown view. Reconstruction based on the holotype, lingual side completed from Rs 908.50. (*b*), (*c*) P^4, lingual and crown views, Rs 553.48. ×6.

P^3 is a small, triangular tooth with three roots. The buccal part of the crown is occupied by the paracone, from which a metastylar crest runs to the postero-buccal apex. The protocone is on the anterior part of the lingual lobe, and behind it is a ledge which represents a very rudimentary hypocone. There is a small parastyle.

P^4 resembles that of *A. edwardsi*. There is a high paracone, and a well-developed metastylar shearing crest. The lingual lobe is relatively small and occupies a lesser proportion of the width of the crown than in *Erinaceus* or *Gymnurechinus*. It bears a small protocone, and a lower, and slightly more lingual, hypocone. There is a small parastyle, connected by a cingulum to the protocone, but the buccal cingulum is absent. In Rs 908.50, P^4, P^3 and the canine are incompletely erupted, although all three molars are fully in place.

M^1 is present only in the holotype, in which its lingual border is not exposed. It differs from *A. edwardsi* in the greater development of the metastylar shear. The postero-buccal apex of the tooth projects slightly outwards, so that there is a bay in the buccal edge. The metacone is slightly higher than the paracone; the two cusps meet at the base well above the level of the buccal cingulum; there is a small metaconule, immediately lingual to the metacone.

M^2 is present in Rs 908.50 and the holotype. Its buccal edge is oblique, the metastylar shearing crest being greatly reduced; a small metaconule is again visible; there is a short lingual cingulum ledge between the bases of the protocone and hypocone.

M^3 is a small, transverse, two-rooted tooth. On its crown can be made out a parastyle, paracone and protocone, arranged in a transverse row and poorly differentiated from each other; the protocone is the highest cusp.

LOWER TEETH.—I_2 is preserved in the holotype. It is a large tooth whose root extends back internally to the mental foramen and ends below P_4. The root causes a slight swelling of the inner side of the mandible, behind the symphysis, as in *A. edwardsi*. In Rs 1398.50 the root of I_2 is seen in cross-section below the posterior end of P_2. The crown of I_2 is visible only in external view. The shape of the tooth does not suggest persistent growth. Its tip must have occluded with the postero-medial side of I^1 when the jaws were closed.

I_3 is a small, procumbent tooth as in *A. edwardsi*. The lower canine is also procumbent, but is relatively larger than in *A. edwardsi*, being twice as long as I_3 and correspondingly more elevated. It resembles the canine of *A. edwardsi* in shape. P_3 is a procumbent tooth, similar to I_3 in size and shape of crown. In the holotype it possesses two roots, close together, the posterior root displaced lingually; this is also true of Sgr 319.49. In Rs 553.48 alveoli for two roots of P_3 are present, but both are in line; in Rs 1398.50 only the posterior root is preserved, but again it is in line. P_3 has only one root in European species of *Amphechinus*.

In buccal view, P_4 resembles that of *A. edwardsi*: the paraconid is high and anterior in position. The lingual side cannot be seen in the holotype, but Rs 553.49 (Text-fig. 17; Pl. 4, fig. 31) shows that the metaconid, though closely united with the base of the protoconid, is moderately distinct, resembling specimens of *A. arvernensis*. The buccal cingulum is extremely faint in the holotype, and absent in Rs 553.49. P_4 is a little shorter in proportion to M_1 than in *A. edwardsi*. In Sgr 319.49 the alveoli of P_4 indicate a somewhat longer tooth.

The crown of M_1 is fully visible only in Rs 1398.50, in which, however, it is somewhat weathered. The paraconid is anterior in position, as in other species of *Amphechinus*. The protoconid is much higher than the hypoconid. A buccal cingulum is present in the holotype.

M_2 is a little longer in proportion to M_1 than in *A. edwardsi* (the length of M_2 is 82% of that of M_1, as compared with 73% in *A. edwardsi* and 86% in *A. intermedius*. Table 7). The paraconid is relatively a little larger than in Recent Erinaceinae. A buccal cingulum is present in the holotype. M_3 is a small tooth with one root.

Relationships.—Several characters show that *A. rusingensis* belongs to *Amphechinus* rather than *Gymnurechinus*: I^1 enlarged; premaxilla forms half the length of the snout in front of the infraorbital foramen; P^4 partly below orbit; palatal vacuities well developed; lingual part of P^4 relatively small; I_2 root extending beyond P_2.

The genus *Amphechinus* has a wide range in space and time. The smallest species, *A. minimus* and *A. kansuensis*, occur in the Oligocene of China (Bohlin 1942). *A. minimus* is atypical in that M_2 is relatively large in proportion to M_1, the metaconid of P_4 is more distinct than usual, and the posterior part of the jaw is somewhat more elevated. It is placed in the genus mainly because I_2, judging from the crushed alveolus, is relatively large. *A. kansuensis* resembles *A. edwardsi* in the degree of elevation of the posterior end of the jaw. It is specialized in that the lower canine is greatly reduced, its alveolus being smaller than that of I_3. *A. acridens* (Matthew & Granger 1924), also from the Oligocene of East Asia, is the next largest species. It is primitive in the frequent presence of a second root on M_3, in the development of the talonid of M_3 and in the partial division of the root of P_2. *A. rectus* (Matthew & Granger 1924) is comparable in size with the European *A. arvernensis*. A specimen referred to this species by Bohlin (1937) possesses a groove on the outer side of the root of I_2, apparently not found in any other member of the genus.

The oldest European specimens are referred to *A. cayluxi* (Filhol), from the Lower Stampian. In the Upper Stampian occurs the very similar *A. arvernensis* (de Blainville), and in the Aquitanian *A. edwardsi* (Filhol). Viret (1929, 1938) and Lavocat (1951) suggested that these three forms should be united as a single species; they are undoubtedly closely allied. It seems unlikely, however, that a species of mammal should have persisted so long without change, and an intensive study, aided by statistical analysis, might well reveal significant differences. At present it is unknown whether such differences as exist (cf. Butler 1948) are of taxonomic value. Examination of the holotype of *A. arvernensis* showed that, whereas the skull is only about 5% smaller than the holotype of *A. edwardsi*, the molar teeth are proportionately more reduced in buccal length, the reduction becoming more marked towards the posterior end of the series. The Aquitanian *Dimylechinus bernoullii* Hürzeler might have arisen by a continuation of this trend to the point where M^3 is lost altogether. This would imply that *A. arvernensis* is not directly ancestral to *A. edwardsi*, but is specialized in a different direction. In other respects *A. arvernensis* is slightly the more primitive of the two forms: its average size is smaller; P^2 is larger, and apparently always has two roots, whereas in *A. edwardsi* it is often one-rooted; M^1 and M^2 are more transverse; the metaconid of P_4 is more distinct.

Erinaceus pomeli Schlosser (1925), from the Stampian, may be identical with *A. arvernensis*: the presence of only two roots on P^3 of an erinaceine of this date seems most unlikely, and it would probably be better to regard the three teeth as P^3, P^2 and C, instead of P^{4-2}.

A. intermedius, from the Lower Sarmatian, is the last and also the largest European species. It differs from the earlier species in that the posterior part of the jaw is more elevated, implying that the glenoid facet was also more elevated in relation to the teeth, as in Recent Erinaceinae. It also approaches the modern forms in that M_2 is relatively large in comparison with M_1 (length M_2/length M_1 0·86). It apparently shares both of these characters with *A. minimus*. As was pointed out by Bohlin (1942), some of the specimens referred by Gaillard (1899) to *Erinaceus sansaniensis* seem to be referable to another species of *Amphechinus*, resembling *A. edwardsi* in size but *A. intermedius* in the elevation of the posterior end of the jaw. Viret (1929) referred some of the specimens of *Erinaceus priscus* figured by Schlosser (1888) to *Amphechinus*, but said that other specimens represent "un *Erinaceus* vrai, reconnaissable au coude brusque de la branche montante de la mandibule". Without the evidence of the incisors, there is no reason why these specimens should not represent an *Amphechinus* of the *A. intermedius* group. *A. robustus* (Lavocat, 1951) probably does not belong to this group because its M_2/M_1 ratio is only 0·79; the posterior part of its jaw is unknown.

A. rusingensis occupies an isolated position in the genus. In spite of its comparatively late date, it retains a number of primitive characters: the large size of the canines; the division of the root of P_2 (approached by *A. acridens*); the distinct metaconid of P_4 (resembling *A. minimus* and *A. arvernensis*); the relatively large M_2 (exceeded by *A. minimus* and *A. intermedius*). The backwardly sloping coronoid process distinguishes it from the *A. intermedius* group. The strong metastyle of M^1, the longer nasals, the lower interorbital region, and the weaker frontal crests, distinguish it from *A. edwardsi*. It seems likely that several lines of evolution are comprised in the genus *Amphechinus*, and that when more is known of the skulls of the various species it will be necessary to subdivide the genus.

THE PHYLOGENY OF THE ERINACEINI.—So long as the earlier members of the Erinaceini were all referred to *Amphechinus* (=*Palaeoerinaceus*), it was natural to suppose that the Recent forms had been derived from that genus. Only in *A. edwardsi* is the skull adequately known, and although it was shown by Viret (1938) to differ from *Erinaceus* in a great many ways, these are nearly all in the direction of the Echinosoricinae and presumably are primitive characters. The enlarged anterior incisors provide an exception. Bohlin (1942) showed that such enlarged incisors are common to the species of *Amphechinus* and are a specialized generic character. It is not impossible, however, that these teeth should have been secondarily reduced in size in the evolution of the modern forms. Another character of *Amphechinus* emphasized by Bohlin is the reduced size of the second and third molars in comparison with P^4. This seems to be associated, at least in *A. edwardsi*, *A. arvernensis* and *A. rusingensis*, with the posterior displacement of the cheek teeth in relation to the orbit. The character is less developed in some species than in others; *A. intermedius* in particular approaches the Recent Erinaceinae. If the series *A. arvernensis*, *A. edwardsi*, *A. intermedius* represents the trend of advance, it would seem to be in the direction of *Erinaceus*. There is also an advance towards the modern forms in some details of the lower jaw (Butler 1948), and by Sarmatian times the jaws of *Erinaceus* (sensu lato) and *Amphechinus* are almost identical.

The discovery of *Gymnurechinus* necessitates a revision of this view. *Gymnurechinus* is an exceedingly primitive erinaceine, in some respects, e.g., the relatively larger canines, more primitive than *Amphechinus edwardsi.* Yet it already resembles the modern Erinaceinae in the small size of the incisor teeth, the proportionate lengths of the molars, and the development of the lingual cusps of P^4. It is therefore unnecessary to suppose that these characters of *Erinaceus* have been derived by reversal of evolution from the more advanced characters of *Amphechinus*, and Viret's view (1938, 1940) that *Erinaceus* and *Amphechinus* represent divergent lines of evolution is confirmed. It still remains necessary to believe that in some ways *Amphechinus* was acquiring by parallel evolution characteristics of *Erinaceus* such as the palatal perforations, the elevation of the posterior end of the mandible, and the union of the roots of P_2.

Friant (1934*b*, 1950) laid emphasis on the metaconule of the upper molars, which, she maintained, is present in *Erinaceus* but absent in *Amphechinus.* This cusp is very poorly developed in Erinaceini, and can be distinguished only on unworn teeth. It is not unknown in *Amphechinus* (Viret 1938, 1940), and is present in *A. rusingensis.* It is developed on unworn molars of all three species of *Gymnurechinus.* Viret doubted whether such a small cusp, easily removed by wear, could be homologous with the metaconule, which is normally visible even in worn teeth. A more typical metaconule occurs in *Galerix, Neurogymnurus* and *Proterix,* and it is probably an ancestral feature of the Erinaceini. The small transient cusp in the position of the metaconule is more likely to be a vestige of a once more definite cusp than a new development, just as the similar elevation of the protocone-paracone crest can be considered as a relic of the protoconule. It is doubtful whether structures in process of reduction are of much taxonomic value.

Pairó and Villalta (1947) described a hedgehog from the Pontian of Spain, which they called *Palerinaceus* (*Postpalerinaceus*) *vireti.* Accepting Viret's view that *Amphechinus* ("*Palerinaceus*") is not ancestral to the modern hedgehogs, they regarded their new species as a late survivor of the *Amphechinus* lineage which had acquired many of the characters of *Erinaceus* by parallel evolution. They listed 36 characters which this form shared with *Amphechinus edwardsi*, against eleven shared with *Erinaceus.* The characters shared with *Amphechinus* are almost entirely primitive characters found also in *Gymnurechinus*, e.g. the horizontal zygoma, the position of the glenoid fossa near the plane of the teeth, the correspondingly low condyle of the mandible, and the backwardly sloping, rather broad coronoid process. Other primitive characters are the entepicondylar foramen of the humerus, the relatively low protoconid and paraconid of P_4, and the shape of the trigonids of the lower molars. In the relatively large upper canine, *P. vireti* resembles *Gymnurechinus* and *Amphechinus rusingensis.* In the long nasals, which reach the level of the postorbital processes, and the low foramen magnum, which does not rise to the level of the top of the condyles, *P. vireti* resembles *Gymnurechinus.* Specialized characters of *Amphechinus* are absent: the anterior incisors are not more enlarged than in *Erinaceus,* P^4 is placed in front of the orbit, there is no evidence of shortening of the posterior part of the palate and the mid-cranial region, P^4 is shorter than M^1 and broader than long, with well-developed lingual cusps, and M_2 is longer in proportion to M_1 than it is in *A. edwardsi*. Therefore there seems no reason for placing this species in the genus *Amphechinus*, and *Postpalerinaceus* should be raised to generic rank.

Postpalerinaceus possesses several features characteristic of the modern Erinaceinae: short snout; broad external nares; simple condyles; frontals swollen by the posterior extension of the olfactory chamber; I^2 displaced inwards; I^3 not much longer than broad; P^3 greatly reduced and simplified. The presence of a basisphenoidal pit seems to be indicated in the figure, but not specifically mentioned in the text, where it is stated merely that the basisphenoid and basioccipital are nearly in the same plane. *Postpalerinaceus* is probably best regarded as a conservative member of the *Erinaceus* lineage. It possesses some specialized features, notably the broadening of the brain-case, the great prominence of the mastoid process, and the strong development of the anterior lambdoid crest.

Mioechinus oeningensis (Lydekker), from the late Middle Miocene (Tortonian) of Europe, has also been interpreted (Butler 1948) as intermediate between *Amphechinus* and the Recent Erinaceinae. It is known only by the palatal view of the skull. It is primitive in the shape of the occipital condyle and in the relatively elongated P^4. The upper surface of the specimen shows a deep and relatively large parafloccular fossa, 3·2 mm. in diameter. Some of the characters of *M. oeningensis* ally it with *Erinaceus*: there is a shallow but definite basisphenoidal pit; the snout is abbreviated; I^2 is displaced lingually, owing to crowding of the incisors; the canine is smaller than I^3; P^3 is crowded and reduced. The main character shared with *Amphechinus edwardsi* is the shortening of the middle part of the skull. This is particularly marked in the region between the palate and the auditory bulla: compared with *Amphechinus*, this region is shorter in proportion to transverse measurements. The zygoma arises opposite M^1 as in *Amphechinus*, so that the cheek teeth are probably displaced backward in relation to the orbit, but the molar region of the palate has not been appreciably reduced in length, and although M^2 is smaller in proportion to M^1 and P^4 than in *Gymnurechinus* and *Erinaceus*, it is larger than in *Amphechinus edwardsi* and *A. rusingensis*. Moreover, the lingual part of P^4 is better developed than in *Amphechinus*. The root of I^1 measures 2·2×1·6 mm., and is not proportionately larger than in *Gymnurechinus*. The total length of the incompletely preserved tooth is 16 mm.; in *A. edwardsi*, with a skull about one-fourth smaller, the total length of I^1 is 18 mm. Although the position of *M. oeningensis* remains doubtful, it is probably best to regard it as a member of the *Erinaceus* lineage which has paralleled *Amphechinus edwardsi* in the reduction in length of the middle part of the skull.

Mioechinus sansaniensis, from the Vindobonian of Europe, is known almost exclusively by lower jaws (Depéret, 1887; Gaillard, 1899; Stromer, 1928; Butler, 1948). It differs from *Amphechinus* in the smaller size of I_2, which does not extend back beyond P_2. The posterior part of the jaw is elevated, but this does not distinguish this species from *Amphechinus intermedius*. The specimens differ considerably in size, and may represent more than one species. There is no evidence of special relationship to *Mioechinus oeningensis*, the lower jaw of which is unknown, and the generic reference is uncertain. If *M. sansaniensis* is compared with *Gymnurechinus leakeyi*, a number of differences are noted. In *Gymnurechinus* the antemolar part of the jaw is much longer, the canine and P_2 are larger, the latter having two roots, and the posterior part of the jaw is much less elevated. The humerus referred to *M. sansaniensis* by Depéret has lost the entepicondylar foramen. If *G. leakeyi* is Lower Miocene in date, the time available seems too short to bridge the gap that separates it from *M. sansaniensis* in the Middle Miocene.

Still older than *Mioechinus sansaniensis* is *M. butleri* Crusafont, Villalta & Truyols (1955), from the Burdigalian of Spain, thus contemporaneous with *Gymnurechinus*. Only its upper cheek-teeth are known. It differs from *Amphechinus* and resembles *Gymnurechinus* and *Erinaceus* in the relatively large size of M^2 and in the quadrate form of P^4, the lingual lobe of which is well developed. However, in comparison with *Gymnurechinus*, P^4 of *M. butleri* is less compressed anteroposteriorly, M^3 is more reduced, and P^3–M^2 possess a much more marked incisure in the posterior border of the crown; moreover there is a complete lingual cingulum on M^1 and M^2. M^1 is only slightly broader than long, as in *G. camptolophus*, and a hypocone is present on P^3, as in *G. songhorensis*.

The Middle Tertiary Erinaceinae thus appear to fall into two groups, one containing *Amphechinus* and *Dimylechinus*, the other *Gymnurechinus*, *Mioechinus* and *Postpalerinaceus*. The ancestry of the Recent Erinaceinae must be sought in the second group. Whereas *Amphechinus* can be traced back well into the Oligocene, the *Erinaceus* lineage appears in the geological record in the Lower Miocene, and its Oligocene predecessors remain to be discovered.

Sub-family ECHINOSORICINAE

Genus *GALERIX* Pomel, 1848.

Galerix africanus sp. nov.

(Plate 4, figs. 37, 38; Text-fig. 18.)

Diagnosis.—A species of *Galerix* that resembles *G. exilis* rather than *Pseudogalerix stehlini* in the relative sizes of P_3 and P_4, and in the development of the metaconid of P_4, but differs from *G. exilis* in the more independent paraconid of P_4. Much larger than *G. exilis* (P_3–M_2 11·0 mm.).

Holotype.—Sgr 315.49, a fragment of mandible containing P_3 and P_4, from Songhor.

Referred Material.—Rs 1201.47, a mandibular fragment with worn M_2, from Hiwegi, Rusinga Island, agreeing in size with the alveoli present in the holotype.

Description.—The holotype is a piece of lower jaw with P_3 and P_4, and the alveoli of P_2, M_1 and M_2. The referred specimen shows M_2 and the alveoli of M_3. It is placed in the same species because the parts that can be compared agree closely in size and proportions with the holotype. The two specimens indicate that the jaw was about 25% larger than in *G. exilis*, and comparable in size with *Pseudogalerix stehlini* (Table 16).

The lower border of the horizontal ramus is nearly straight, but begins to rise below M_3, and the angular process must have been a little higher than in *G. exilis*, only slightly below the level of the teeth. The anterior edge of the coronoid process also rises more steeply than in *G. exilis*. The anterior end of the masseteric fossa is visible in Rs 1201.47. On the lingual side, a crest runs backwards and upwards from the base of the coronoid process, as in *G. exilis*. On the holotype it may be seen that the symphysis ends below P_3, and the mental foramen opens below the anterior part of P_4.

P_2, of which only the posterior alveolus is preserved, must have been about as long as P_3. P_3 is relatively broader than in *G. exilis* and *P. stehlini*; the posterior part is broader than the anterior part, so that its outline approaches a triangle, whereas in both the European species it is oval in outline. There is no trace of the metaconid, but a small anterior basal cusp is present, and posteriorly there is a cingulum-like talonid which bears a small posterior cusp. P_4 is higher and longer than P_3, but the difference is not so great as in *Pseudogalerix*: the proportionate heights and lengths of the two teeth are similar to *G. exilis*. The protoconid of P_4 is high and trigonal; the metaconid resembles that of *G. exilis*, and is much better developed than in *Pseudogalerix*; the paraconid is more independent and conical than in *G. exilis*, and resembles that of *Pseudogalerix*, though it is relatively higher; the talonid resembles that of P_3. A faint cingulum is present on the buccal side of the paraconid, but it does not extend back to the protoconid. Judging by the alveoli, M_1 was longer and broader than P_4, as in *G. exilis*. M_2 of specimen Rs 1201.47 closely resembles *G. exilis* and *Pseudogalerix*, but it differs from these in being larger in proportion to P_4. The paraconid is reduced; the protoconid and hypoconid are more worn than the metaconid and entoconid; the protoconid is higher than the hypoconid, but the metaconid is equal in height to the entoconid; the metaconid is slightly more

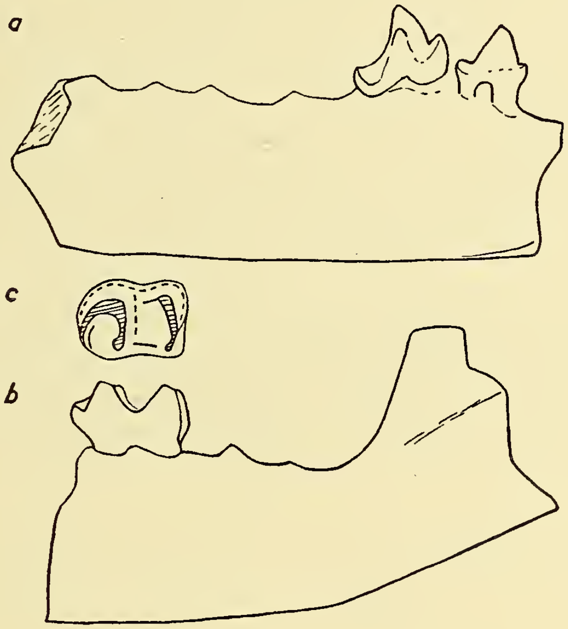


FIG. 18. *Galerix africanus*. (*a*) Lingual view of the holotype, with P_3 and P_4. (*b*) Rs 1201.47, buccal view, showing M_2. (*c*) Crown view of M_2 of Rs 1201.47. ×5.

anterior than the tip of the protoconid; there is a continuous buccal cingulum from the paraconid to the hypoconulid, which is midway along the crest joining the hypoconid to the entoconid; there is no lingual cingulum. M_3 has two roots, but is much smaller than M_2. The alveoli of M_1 and of M_2 are connected by a short groove, as in other Erinaceidae.

RELATIONSHIPS.—This species clearly belongs to the Galericini, of which it is the first African representative to be discovered, but in view of the fragmentary nature of the material, its generic reference must be regarded as provisional. It agrees with *Galerix exilis* rather than with *Pseudogalerix stehlini* in the metaconid of P_4 and in the relatively large size of P_3, but it shows an approach to *Pseudogalerix* in the paraconid of P_4. If Rs 1201.47 is correctly referred to this species, M_2 would seem to be larger in proportion to M_1 than in the European species.

Neurogymnurus minor Filhol should be referred to the genus *Tetracus*, and not to *Galerix* (Lavocat 1951; cf. Butler 1948). *Tetracus* resembles *Pseudogalerix* rather than *Galerix* in the reduced size of P_3 and of the metaconid of P_4, and perhaps also in the more upright canine. The proportionate sizes of P_4–M_3 are nearly the same as in *Pseudogalerix* and *Galerix exilis*; P_3 is relatively a little broader and not so much reduced as in *Pseudogalerix*. *Tetracus* may be ancestral to *Pseudogalerix*.

Ictopidium lechei Zdansky (1930), from the Oligocene of China, should also be placed in the Galericini. It is clearly not a leptictid, because of the non-molariform character of P_4. It resembles *Galerix exilis* and *G. africanus* in the pattern of M_2 and in the development of the metaconid of P_4. P_3 is broad posteriorly, as in *G. africanus*. The proportions and relative sizes of P_3 and P_4 are very similar to *G. africanus*, but M_1 and M_2 are smaller in proportion to the premolars (Table 16). M_3 is nearly as long as M_2, a character shared with *Tupaiodon*, which *Ictopidium* also resembles in the relatively small lower canine.

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Table 1

PROPORTIONS OF ERINACEID SKULLS

Measurements expressed as ratios of the width of the palate across the paracones of M^1

	Echinosorex gymnurus	*Hylomys suillus*	*Neurogymnurus cayluxi**	*Gymnurechinus leakeyi*	*Amphechinus edwardsi*†	*Hemiechinus auritus*	*Erinaceus europaeus*
Snout anterior to P^4 . . .	0·90	0·78	0·85	0·81	0·77	0·62	0·71
Anterior end of P^4—palatal crest .	1·01	0·82	0·77	0·72	0·70	0·76	0·81
Palatal crest—eustachian canal .	0·64	0·52	0·58	0·62	0·51	0·60	0·59
Eustachian canal—foramen magnum	0·66	0·56	0·75	0·73	0·60	0·62	0·49
Greatest postglenoid width . .	1·18	1·24	1·47	1·39	1·24	1·37	1·29
Across condyles	0·66	0·69	0·71	0·62	0·59	0·63	0·59
Height of posterior end of skull .	0·89	0·85	1·00	0·85	0·80	0·65	0·71

* Type of *Cayluxotherium elegans* Filhol.
† Holotype; length of snout from Viret (1938, fig. 6).

Table 2

MEASUREMENTS OF SKULLS OF *GYMNURECHINUS*

	G. leakeyi				*G. camptolophus*		*G. songhorensis*		
	Rs 12.32	Rs 491.51	Rs 1.49	Rs 402.50	Rs 424a.48	Rs 424.48	Sgr 513.49	Sgr 62.47	Rs 32a.32
Across first molars at level of paracones . . .	16·3	16·5			18·7			18·7	
Anterior end M^1—anterior end of canine	11·3	11·1	11·5		12·3			12·0	
Lachrymal foramen—tip of snout		17·5e			21·5	21·0		21·0	
Anterior end P^4—tip of snout		13·0e			15·2			16·6	
Anterior end P^4—palatal crest	12·3	12·5	12·5		14·8				
Across canines . . .	8·7	8·5			9·8			9·7	
Palatal crest—upper surface of frontal	13·3	13·1	13·5		14·0				
Between lachrymal foramina .	15·2	14·2	14·0e		15·8	16·0		16·7	
Across postorbital processes .	13·3	13·5	13·2e		13·9	14·0		14·9	
Minimum width mid-cranium	10·8				11·1	11·3	11·2	11·0	
Across zygomata . . .	30·0					35·0		32·0e	
Lachrymal foramen — post-glenoid process . . .	24·0		23·5		27·5	27·2		27·6	
Palatal crest—foramen ovale .	10·8		10·5		11·5				
Foramen ovale—posterior end of condyle . . .	16·0		16·3		16·8		14·3	14·0e	
Across condyles . . .	10·2		10·3		11·2e		11·2	11·5	
Across post-tympanic processes	22·7		22·5	22·4	22·0e		22·0	23·0	
Across paroccipital processes	16·5		16·7e	17·1	17·0e		16·5	16·0	16·4
Occipital height . . .	13·8		15·0e			16·0	13·3e	14·0	13·0e

In this and other tables all measurements are in millimetres. e=estimated measurement.

TABLE 3

MEASUREMENTS OF LOWER JAWS OF *GYMNURECHINUS*

	G. leakeyi			*G. camptolophus*			*G. songhorensis*
	Rs 12.32	Rs 864.50	Rs 1971.50	Rs 424.48	Rs 564.48	Rs 595.48	Sgr 62.47
Alveolar length M_1–M_3 .	10·0	10·8		11·4	11·0		11·3
Between I_2 and M_1 .	9·8		9·0	11·8	11·0	11·2	10·7
Anterior end—base of coronoid process .				25·0	23·5		25·6
Internal depth at M_1 .	6·0e	6·4	5·2		6·2	6·7	
Base of coronoid process —condyle . . .	15·6			18·5			16·2
Base of coronoid process —tip of angular proc.	15·8			18·0			16·2
Maximum depth posterior end	17·5e			18·5e			19·0
Width of condyle . .	3·8			4·0			4·2
Anterior end — tip of angular process . .	36·0e			43·0			41·0

e=estimated measurement.

TABLE 4

MEASUREMENTS OF UPPER CHEEK-TEETH

	Gymnurechinus leakeyi				*Gymnurechinus camptolophus*	*Gymnurechinus songhorensis*	*Amphechinus rusingensis*
	Rs 828.47	Rs 12.32	Rs 491.51	Rs 111.51	Rs 424a.48 & Rs 424b.48	Sgr 452.48	Rs 723.47
Width of palate across M^1 . .	16·8e	16·3	16·5	16·4	18·7	18·7e	12·2
P^3: buccal edge .	2·2	2·0	1·9		2·6	2·8	1·8
width across paracone . .	2·0		2·1		2·2	2·2	1·2
P^4: buccal edge .	4·1	3·7	3·7	3·8	4·6	4·3e	2·9
width across paracone . .	3·9		3·3		4·3	3·5	2·5
length across waist	2·9	2·6	2·6		3·3	2·8	1·5
M^1: buccal edge .	4·2	3·9	3·9	4·1	4·7	4·9	3·0
anterior width .	4·8		4·5	4·6	4·8	4·9	3·1e
length across waist	3·7	3·3	3·6		4·0	4·3	2·1
M^2: buccal edge .	3·6	3·5	3·4	3·6	3·8		2·2
anterior width .	4·7				4·3		2·5
length across waist	2·9	2·9	2·9		3·4		1·6
M^3: greatest width .			2·9	2·8			1·6

e=estimated measurement.

TABLE 5

MEASUREMENTS OF CHEEK TEETH, AS PERCENTAGES OF PALATAL WIDTH

	Gymnurechinus leakeyi			*Gymnurechinus camptolophus* Rs 424a, b.48	*Gymnurechinus songhorensis* Sgr 452.48	*Amphechinus rusingensis* Rs 723.47	*Amphechinus edwardsi*	*Amphechinus arvernensis*	*Mioechinus oeningensis*	*Hemiechinus auritus*	*Erinaceus europaeus*
	Rs 12.32	Rs 491.51	Rs 111.32								
P^3: buccal edge . .	12·3	11·5		13·9	15·0	14·8	13·0		11·8	11·0	11·2
width across paracone . . .		12·7		11·8	11·8	9·8	10·5		10·8	10·4	11·7
P^4: buccal edge. .	22·6	22·4	23·2	24·6	23·0e	23·8	23·4	25·0e	21·7	21·3	20·3
width across paracone . . .		20·0		23·0	18·7	20·6	20·4		19·2	20·1	20·3
length across waist .	16·0	15·8		17·7	15·0	12·3	13·0		14·8	15·8	13·7
M^1: buccal edge .	24·0	23·6	25·0	25·2	26·2	24·6	21·5	19·6	23·6	25·6	23·8
anterior width .		27·3	28·0	25·7	26·2	25·0e	23·8	25·7	26·1	28·6	24·4
length across waist .	20·2	21·8		21·4	23·0	17·2	17·2	17·6	18·7	23·2	21·3
M^2: buccal edge .	21·4	20·6	22·0	20·4		18·0	18·5	16·2	18·7	21·4	22·8
anterior width .				23·0		20·5	20·0	21·0	21·2	26·2	25·4
length across waist .	17·8	17·6		18·2		13·1	14·0	14·9	15·8	19·5	20·3
M^3: greatest width .		17·6	17·0			13·1	12·8	12·9	14·3	15·9	16·2

e = estimated.

TABLE 6

MEASUREMENTS OF CHEEK TEETH, AS PERCENTAGES OF THE BUCCAL LENGTH OF P^4

	Gymnurechinus leakeyi				*Gymnurechinus camptolophus* Rs 424a, b.48	*Gymnurechinus songhorensis* Sgr 452.48	*Amphechinus rusingensis* Rs 723.47	*Amphechinus edwardsi*	*Amphechinus arvernensis*	*Mioechinus oeningensis*	*Hemiechinus auritus*	*Erinaceus europaeus*
	Rs 828.47	Rs 12.32	Rs 491.51	Rs 111.32								
P^3: buccal edge . .	54	54	51		56	65	62	58		54	51	55
width across paracone .	49		57		48	51	41	46		50	49	57
P^4: buccal edge . . .	100	100	100	100	100	100	100	100	100	100	100	100
width across paracone .	97		89		93	81	86	88		89	94	100
length across waist . .	71	67	70		72	65	52	58		68	74	67
M^1: buccal edge . . .	102	105	105	108	102	114	104	93	78	109	120	118
anterior width . .	117		121	121	104	114	107	105	103	120	134	120
length across waist . .	90	85	97		87	100	72	76	70	86	109	115
M^2: buccal edge . . .	88	95	92	95	83		76	81	65	86	100	113
anterior width . .	115				93		86	86	84	98	123	125
length across waist . .	71	69	78		74		55	65	59	73	91	100
M^3: greatest width . .			78	78			55	53	51	66	74	80

TABLE 7

MEASUREMENTS OF LOWER CHEEK-TEETH OF ERINACEIDAE

	Gymnurechinus leakeyi Rs 864.50	*Erinaceus europaeus*	*Amphechinus edwardsi*	*Amphechinus rusingensis*	*Mioechinus sansaniensis*	*Neurogymnurus cayluxi*
	l b	l b	l b	l b	l b	l b
P_4	3·5 × 2·1	3·5 × 2·4	2·8 × 2·1	1·9 × 1·5	2·5 × 1·8	3·3 × 2·4
M_1	4·5 × 3·0	5·3 × 3·8	4·4 × 3·0	3·3 × 2·0	4·5 × 2·7	4·3 × 2·6
M_2	3·8 × 2·7	4·5 × 3·4	3·2 × 2·3	2·7 × 1·6	3·8 × 2·4	3·2 × 2·5
M_3	2·6 × 1·7	3·0 × 2·1	1·5 × 1·2		1·8 × 1·2	2·5 × 1·8
	length of $M_1 = 100$					
P_4	78 × 47	66 × 45	64 × 48	57 × 45	55 × 40	77 × 56
M_1	100 × 67	100 × 72	100 × 68	100 × 61	100 × 60	100 × 60
M_2	84 × 60	85 × 64	73 × 52	82 × 48	84 × 53	74 × 58
M_3	58 × 38	57 × 40	34 × 27		40 × 27	58 × 42

Table 8

MEASUREMENTS OF CRANIAL CAVITIES AND BRAIN-CASTS OF ERINACEIDAE

	Gymnurechinus leakeyi	*Echinosorex gymnurus*	*Hylomys suillus*	*Galerix exilis*	*Neurogymnurus cayluxi*	*Erinaceus europaeus*
Maximum dorsal length	27·5	35·0	19·0		29·0	26·2
Length excluding olfactory bulbs	23·0	29·5	16·5	15·5	24·5	22·5
Maximum width across cerebrum	18·0	23·0	12·5	15·0	24·0	22·0
Maximum height of cerebrum	11·0	14·0	8·5		11·0	11·0
Dorsolateral length of cerebral hemisphere	13·5	17·0	10·2	9·8	15·5	14·0
Width across olfactory bulbs	9·3	11·5	7·0	8·2	12·0	13·0
Length of olfactory bulb (dorsal view)	5·5	7·8		5·0		6·0
Length of cerebellum (mid line)	9·0	11·0	6·3	5·0	8·0	7·5
Width across cerebellar hemispheres	12·0	15·0	9·8	9·5	14·5	15·5
Maximum height of hind-brain	11·5	15·0	8·8			12·5
Foramen ovale—internal opening of optic foramen	7·8	10·5				5·2
Across foramina ovalia	10·5	12·5	7·0		14·0	12·0
Width of foramen magnum	7·5	9·3	5·5		8·7	9·1

Table 9

PROPORTIONS OF CRANIAL CAVITIES AND BRAIN-CASTS

	Gymnurechinus leakeyi	*Echinosorex gymnurus*	*Hylomys suillus*	*Galerix exilis*	*Neurogymnurus cayluxi*	*Erinaceus europaeus*
Total length/maximum width	1·58	1·62		1·33		1·29
Length excluding olfactory bulbs/maximum width	1·28	1·28	1·32	1·03	1·02	1·02
Dorsolateral length cerebral hemisphere/maximum width	0·75	0·74	0·82	0·65	0·64	0·65
Median length cerebellum/width cerebellum.	0·75	0·73	0·64	0·53	0·48	0·55
Length olfactory lobe/length of rest of brain.	0·24	0·26		0·32		0·27
Width olfactory lobe/width cerebral hemispheres.	0·52	0·50	0·56	0·55	0·50	0·59
Foramen ovale—optic foramen (internal)/width across foramina ovalia	0·74	0·84				0·43
Median length cerebellum/dorsolateral length cerebral hemisphere	0·67	0·65	0·62	0·51	0·54	0·54

TABLE 10

MEASUREMENTS OF SKULLS TO DETERMINE THE PROPORTIONS OF THE CRANIAL CAVITY

	Gymnurechinus leakeyi	*Gymnurechinus songhorensis*	*Echinosorex gymnurus*	*Hylomys suillus*	*Brachyerix loomisi**	*Neurogymnurus cayluxi†*	*Amphechinus edwardsi‡*	*Hemiechinus auritus*	*Erinaceus europaeus*
a. Dorsal border foramen magnum—suboptic foramen . . .	22·2	21·0	30·0	14·0	15·0	20·5	18·0	17·5	19·4
b. Width of cranium in glenoid region	20·5	20·4	26·2	14·2	17·0	22·0	19·0	19·3	22·4
c. Dorsal border foramen magnum—narrowest part of skull between orbits	26·0	23·5	31·0	15·8	17·7	21·8	20·0	19·9	22·3
Ratio a/b	1·08	1·03	1·14	1·01	0·88	0·93	0·95	0·91	0·87
Ratio c/b	1·27	1·15	1·18	1·11	1·04	0·99	1·05	1·03	0·99

* From published figure of Matthew & Mook (1933).
† Holotype of *Cayluxotherium elegans* Filhol.
‡ Holotype.

TABLE 11

MEASUREMENTS OF SKULLS OF ERINACEIDAE TO DETERMINE THE PROPORTIONS OF THE OLFACTORY CHAMBER

	Gymnurechinus leakeyi	*Echinosorex gymnurus*	*Hylomys suillus*	*Erinaceus europaeus*
a. Tip of snout—suboptic foramen .	31·0	48·5	19·5	37·0
b. Skull length.	53·5	78·0	34·0	56·5
c. Infraorbital foramen—suboptic foramen	16·5	23·0	9·5	22·5
d. Infraorbital foramen—posterior end of skull	39·5	54·0	24·0	40·5
e. Width between lachrymal foramina	14·2	20·5	10·2	16·4
f. Infraorbital foramen—posterodorsal end olfactory chamber . .	11·3	19·5	7·0	16·5
g. Greatest width across posterodorsal part of chamber . . .	10·4	14·5	7·6	15·2
h. Posterior height of chamber . .	11·0	15·8	7·9	14·0
i. Maximum height of cerebral cavity.	11·0	14·0	8·5	11·0
Ratios: a/b	0·58	0·62	0·57	0·65
c/d	0·42	0·42	0·40	0·56
c/e	1·16	1·12	0·93	1·37
f/d	0·29	0·36	0·29	0·41
g/e	0·73	0·71	0·74	0·93
h/g	1·06	1·09	1·04	0·92
h/i	1·00	1·13	0·93	1·27

Table 12

MEASUREMENTS OF ERINACEID SKELETONS

	Gymnurechinus camptolophus	*Echinosorex gymnurus*	*Hylomys suillus**	*Erinaceus europaeus*
Length of skull	57·0e	79·0	34·0	57·0
Width across zygomata	35·0	39·0	18·4	33·0
Palatal width	19·0e	27·0	11·4	19·5
Skull—acetabulum	150·0e	225·0	65·0	170·0
Skull—first rib	37·0e	44·0	14·2e	27·0
Length atlas	8·6	11·0	4·0e	4·8
Length axis spine	14·0	20·8	4·5	9·0
Across spinal canal atlas	6·4	9·7	3·6	7·0
Across transverse processes atlas	13·9e	24·8	7·4	16·0
1st rib—last rib (heads)	62·0	108·0	29·5e	70·5
Longest dorsal spine	14·0e	14·5	5·0e	6·5
Longest rib (curve)	37·5	49·0		50·1
Length of centrum of Th 8	4·0	6·8		4·4
Length of centra Th 5–12	33·0	53·0		36·0
Length manubrium sterni	8·7	12·2	4·3	9·5
Anterior width manubrium sterni	12·0	18·4	6·9	10·6
Thoraco-lumbar vertebrae	96·5	146·0		126·5
Last rib—acetabulum	50·0	78·0	28·7	81·0
Height lumbar vertebrae	10·5	16·5	4·1	10·7
Length sacro-iliac articulation	13·5	23·0		20·5
Ventral length sacrals 1–2	10·8	20·0		11·2
Diameter acetabulum	4·8	7·2	2·5	6·0
Length humerus	33·5e	52·0	16·5	42·0
Minimum width humerus	3·0	4·5	2·0	3·4
Width of lower end of humerus	8·8	13·5	4·7	10·8
Ilium anterior to acetabulum	28·5e	43·0	14·3	31·0
Across neck of ilium	3·5	5·8	2·5	4·0
Length of femur	44·0e	55·0	18·8	41·0
Across greater and lesser trochanters	10·0	15·5	4·2	10·6
Across head of tibia	7·8	12·5		8·5
Length tibio-fibula	45·0e	65·0	27·0	50·5
Minimum width tibio-fibula	2·7	4·5		3·5
Length third metatarsal	17·0?	19·0	7·4	11·2

e = estimated measurement.
* From Anderson (1874).

Table 13

PROPORTIONS OF ERINACEID SKELETONS

(skull—acetabulum 100)

	Gymnurechinus camptolophus	*Echinosorex gymnurus*	*Hylomys suillus*	*Erinaceus europaeus*
Skull length	38·0	35·0	55·0	33·0
Palatal width	12·7	12·0	17·3	11·5
Skull—1st rib	25·0e	19·5	21·5e	15·9
1st rib—last rib	42·0	48·0	45·0e	41·5
Last rib—acetabulum	33·5	34·5	43·5	48·0
Longest rib (curve)	27·0	22·0		29·5
Length humerus	22·0e	23·0	25·0	25·0
Length femur	29·5e	24·0	28·0	24·0
Length tibio-fibula	30·0e	29·0	41·0	30·0
Length third metatarsal	11·3?	8·4	11·4	6·6

e = estimated.

Table 14

PROPORTIONATE MUSCULATURE OF FOUR MAMMALS

	Erinaceus europaeus	*Rattus norvegicus*	*Sciurus carolinensis*	*Felis domesticus*
Body weight	529·0	325·0	323·0	2216·0
Total muscles weighed	24·9 (100)	35·6 (100)	42·7 (100)	339·7 (100)
Jaw muscles	2·31 (9·3)	1·81 (5·1)	2·83 (6·6)	10·5 (3·1)
Epiaxial neck muscles	2·47 (9·9)	1·31 (3·7)	1·14 (2·7)	10·1 (3·0)
Extrinsic muscles of shoulder	5·08 (20·4)	7·70 (21·6)	5·08 (11.9)	54·6 (16·1)
Intrinsic muscles of shoulder and forelimb	6·14 (24·7)	5·07 (14·2)	8·11 (19·0)	69·0 (20·3)
Lumbar muscles	2·03 (8·2)	4·66 (13·1)	5·96 (14.0)	45·4 (13·4)
Muscles of hind limb	6·84 (27·5)	15·10 (42·4)	19·60 (45·9)	150·1 (44·2)
Weighed muscles as % of half body weight	9·4	21·9	26·4	30·7

Weights in grams of muscles on one side of the body. Numbers in brackets give the weights of the muscle groups as a percentage of the total weighed muscle.

Table 15

SKULL MEASUREMENTS OF AMPHECHINUS

	A. rusingensis				*A. edwardsi*		*A. rusingensis* ÷ *A. edwardsi*
	Rs 723.47	Sgr 451.48	Rs 908.50	Rs 1398.50	Holotype	B.M. 11720	
Across M^1 (at paracones)	12·2				16·2		0·75
Palatal crest—anterior end P^4		8·0	8·4		11·3		0·71–0·74
M^3—canine (inclusive)	13·2		13·5		16·5		0·80–0·82
Anterior end P^4—posterior end I^1	8·7				11·2*		0·78
Across canines	6·0				8·3		0·72
Minimum interorbital width		6·8			9·6		0·71
Skull anterior to orbit	11·8				15·9*		0·74
M^3–P^4	8·4				11·5		0·77
Palatal crest—top of frontal		8·9			13·5		0·66
M$_3$–tip of I$_2$	17·5					20·8	0·84
M$_1$–M$_3$	7·0			7·0		9·0	0·78
Between M$_1$ and I$_2$	7·0					8·2	0·85

* Estimated by comparison with drawings of Viret (1938).

Table 16

MEASUREMENTS OF THE LOWER CHEEK-TEETH OF GALERICINI

	Galerix africanus	*Galerix exilis* M 4846	*Pseudogalerix stehlini* M 15810	*Ictopidium lechei* (Zdansky, 1930)
	l b	l b	l b	l b
P$_3$	1·8×1·3	1·6×0·9	1·4×0·9	1·4×0·9
P$_4$	2·4×2·0	2·0×1·2	2·4×1·4	1·7×1·2
M$_1$	3·5× ?	2·8×2·0	3·4×2·3	1·9× ?
M$_2$	3·1×2·4	2·2×1·8	2·5×1·8	1·6×1·4
M$_3$	2·2× ?	1·8×1·3	1·8× ?	1·5× ?
	(Length of P$_4$=100)			
P$_3$	75×54	80×45	58×37	82×53
P$_4$	100×83	100×60	100×58	100×71
M$_1$	146× ?	140×100	142×96	112× ?
M$_2$	129×100	110×90	104×75	94×82
M$_3$	92× ?	90×65	75× ?	88× ?

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EXPLANATION OF PLATES

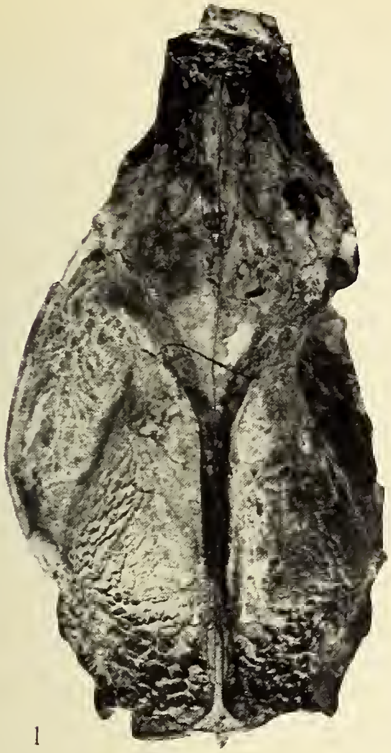
PLATE 1

EXPLANATION OF PLATE I

Gymnurechinus leakeyi

Fig. 1. Rs 12.32. Skull, dorsal view.
Fig. 2. The same, ventral view.
Fig. 3. The same, latero-ventral view, perpendicular to lower jaw.
Fig. 4. Rs 12a.32. Brain-cast, lateral view.
Fig. 5. The same, dorsal view.
Fig. 6. The same, ventral view.
Fig. 7. Rs 1.49. Skull showing brain-cast and cast of interior of olfactory chamber, dorsal view.
Fig. 8. The same, lateral view.

All twice natural size.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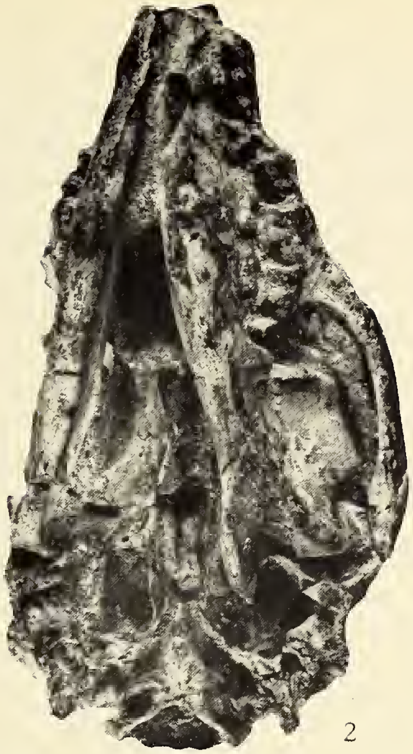
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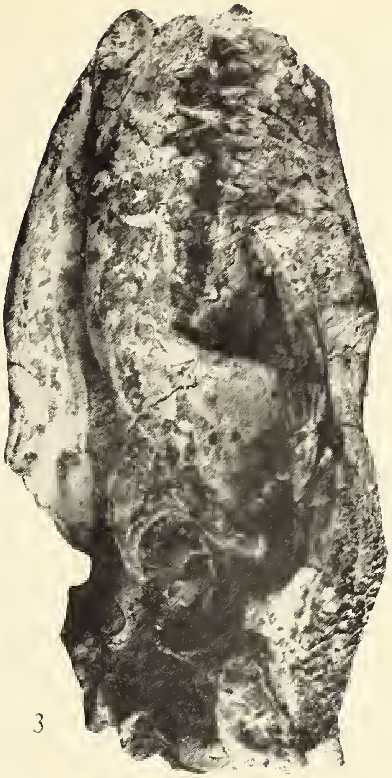
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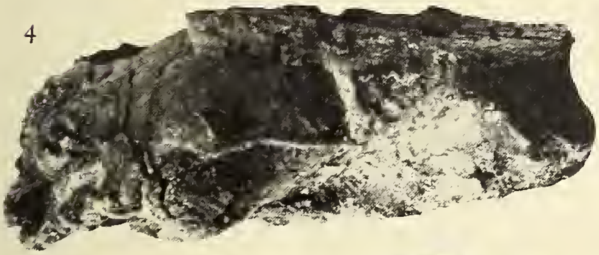
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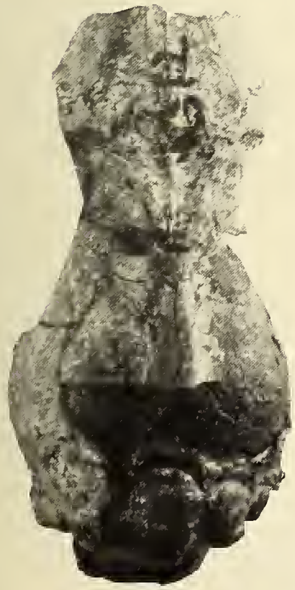
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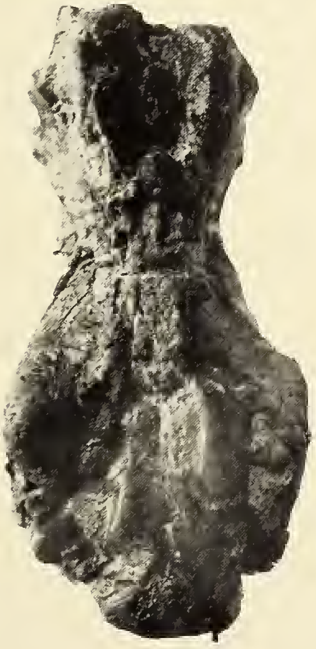
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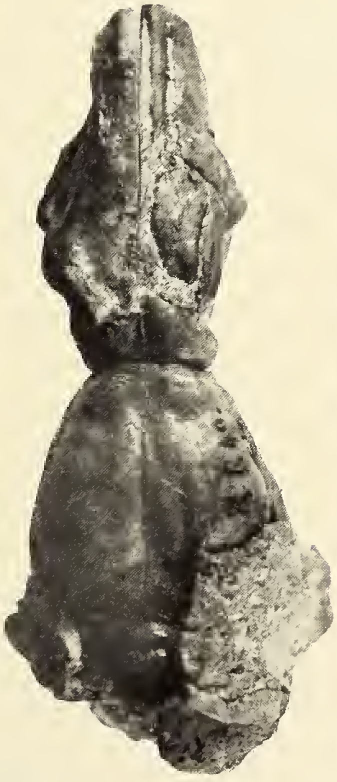
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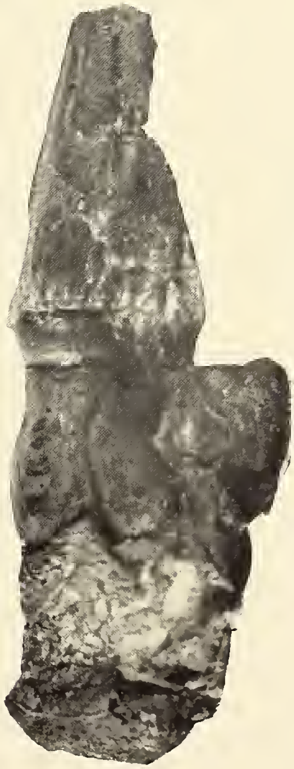
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GYMNURECHINUS LEAKEYI

PLATE 2

EXPLANATION OF PLATE 2

Gymnurechinus camptolophus

FIG. 9. Rs 424a.48. Skull, dorsal view.
FIG. 10. The same, ventral view.
FIG. 11. The same, lateral view.

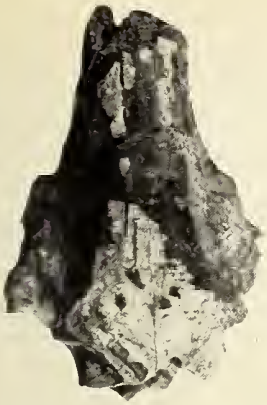
G. leakeyi

FIG. 12. Rs. 491.51. Anterior part of skull, dorsal view.
FIG. 13. The same, ventral view.
FIG. 14. The same, lateral view.
FIG. 15. Rs 864.50. Mandible with P_4–M_3, medial view.
FIG. 16. Rs 1971.50. Mandible with P_2, lateral view.

G. camptolophus

FIG. 17. Rs 564.50. Mandible with C–P_4, medial view.

Figs. 9–14 twice natural size, figs. 15–17 three times natural size.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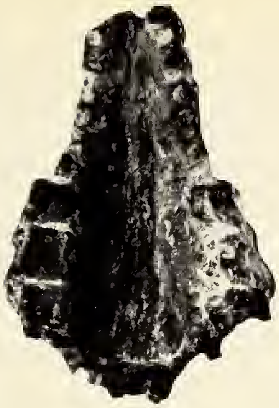
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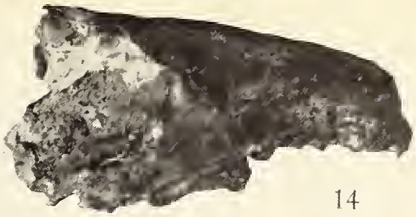
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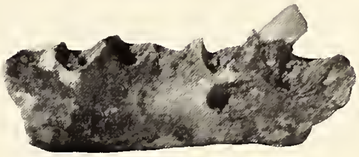
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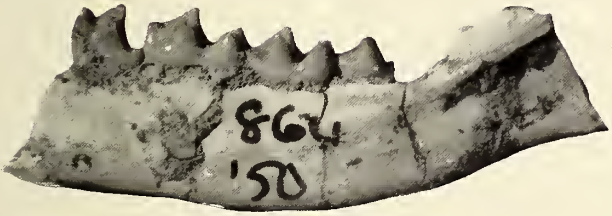

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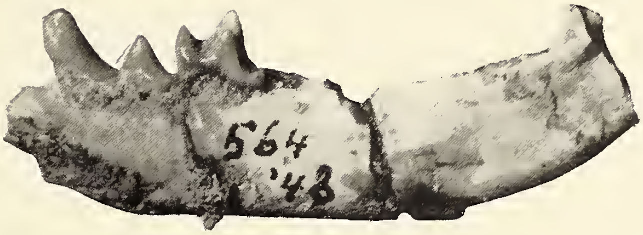

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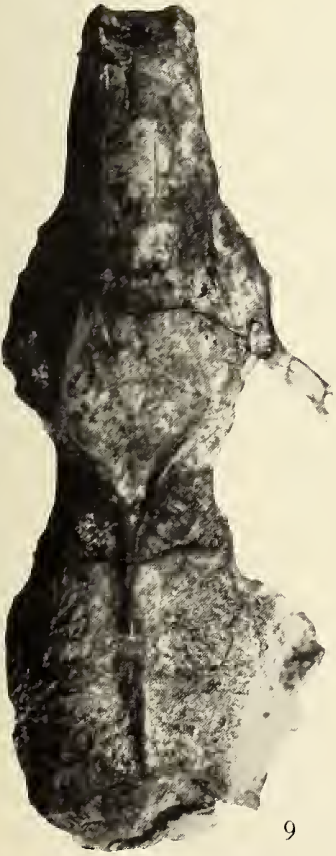
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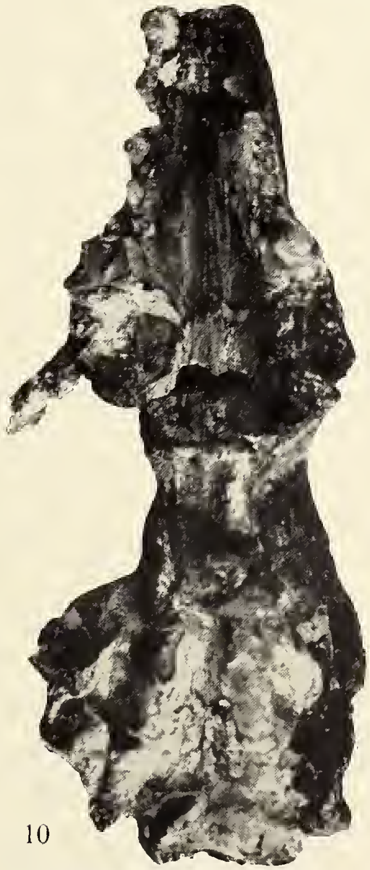
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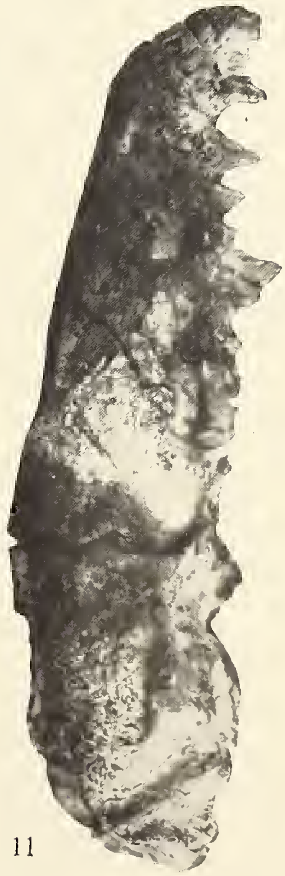
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GYMNURECHINUS

PLATE 3

EXPLANATION OF PLATE 3

Gymnurechinus songhorensis

FIG. 18. Sgr 513.49. Latero-dorsal view. × 1·6.
FIG. 19. The same, posterior view.

G. leakeyi

FIG. 20. Rs 12.32. Latero-dorsal view of cranium. × 1·6.
FIG. 21. The same, posterior view.
FIG. 22. Rs 402.50. Ventral view.

Erinaceus europaeus

FIG. 23. Dorsal view of cranium of old animal. × 1·75.

Gymnurechinus songhorensis

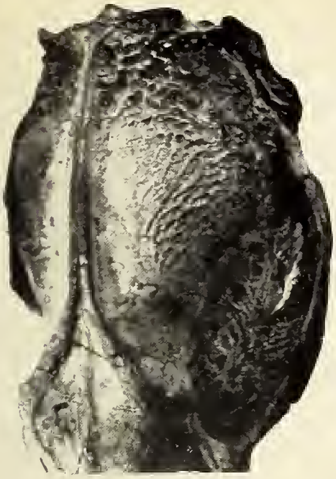
FIG. 24. Sgr 513.49. Dorsal view.
FIG. 25. The same, lateral view.
FIG. 26. The same, ventral view.

Neurogymnurus cayluxi

FIG. 27. B.M. M3752. Latero-dorsal view of cranium.

Except where stated, all twice natural size.

PLATE 3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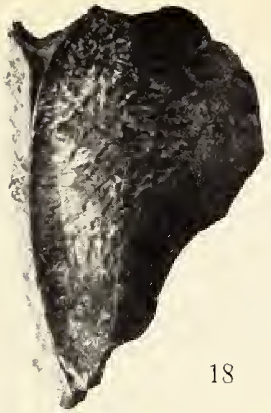
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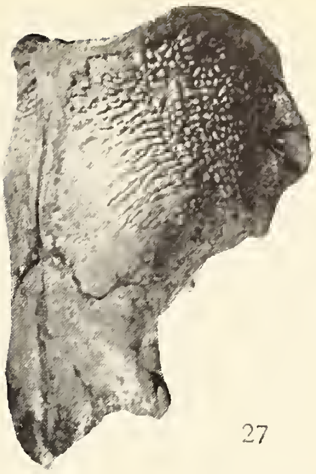
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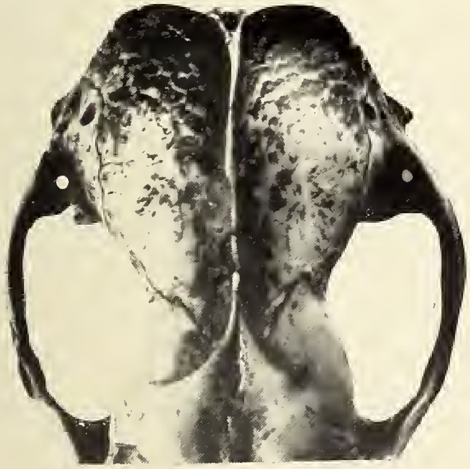
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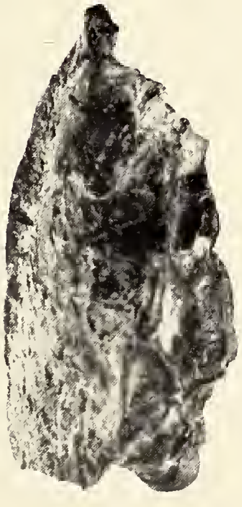
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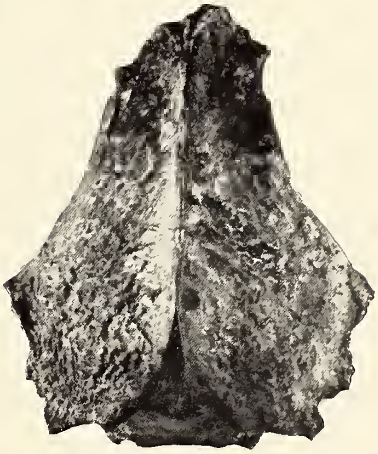
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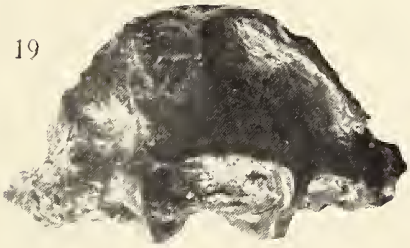

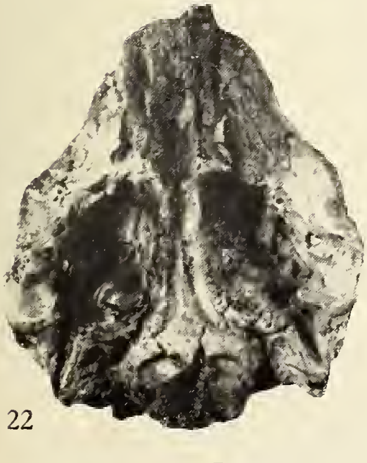
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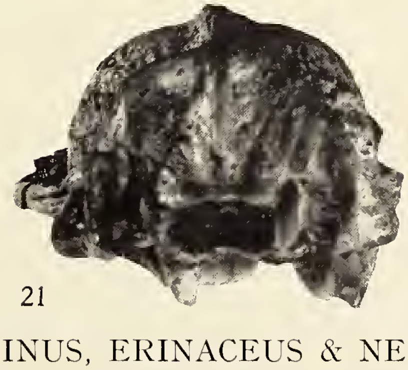
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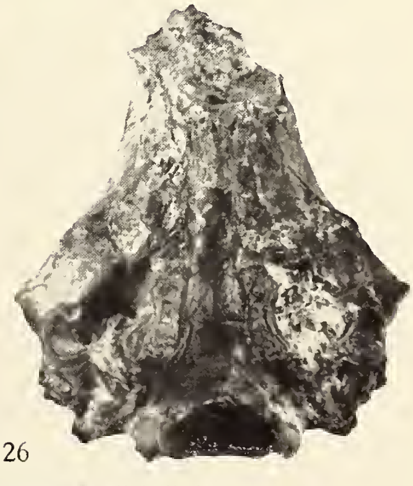
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GYMNURECHINUS, ERINACEUS & NEUROGYMNURUS

PLATE 4

EXPLANATION OF PLATE 4

Amphechinus rusingensis

Fig. 28. Rs 723.47. Skull, lateral view. ×4.
Fig. 29. The same, ventral view. ×4.
Fig. 30. Sgr 451.48. Skull, palatal view. ×4.
Fig. 31. Rs 553.48. Mandibular fragment with P_4, medial view. ×4.

Neurogymnurus cayluxi

Fig. 32. B.M. M9653a. Plaster cast of interior of skull-roof. ×2.

Gymnurechinus leakeyi

Fig. 33. Rs 828.47. P^3–M^2, crown view. ×3.

G. songhorensis

Fig. 34. Sgr 452.48. P^3–M^1, crown view. ×3.

G. camptolophus

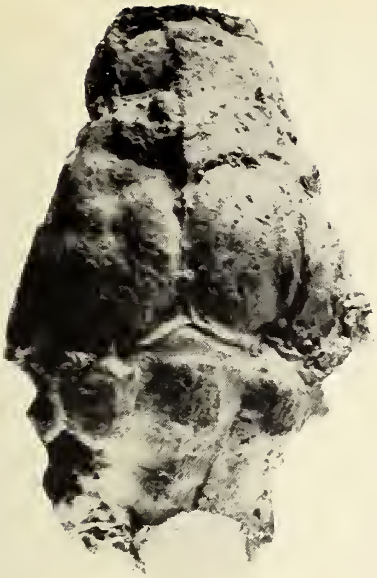
Fig. 35. Rs 424b.48. M^1 and M^2, crown view. ×3.

G. leakeyi

Fig. 36. Rs 864.50. Jaw with P_4–M_3, crown view. ×3.

Galerix africanus

Fig. 37. Sgr 315.49. Mandible with P_3 and P_4, internal view. ×4.
Fig. 38. Rs 1201.47. Mandible with M_2, internal view. ×4.



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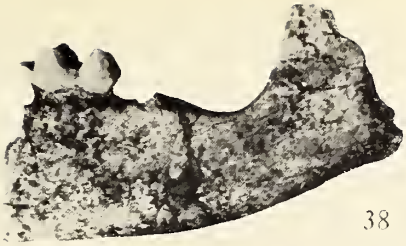

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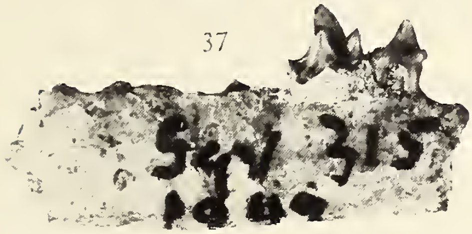

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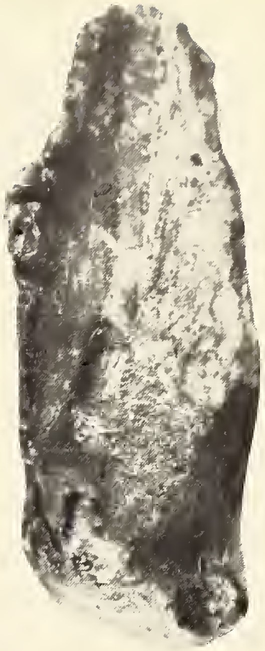

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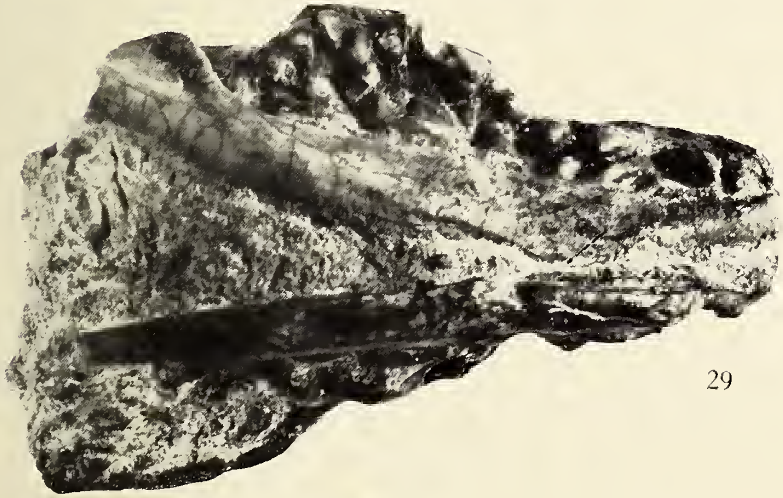

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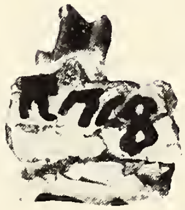

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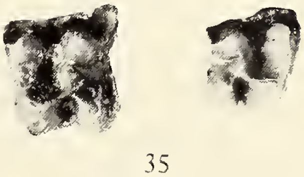

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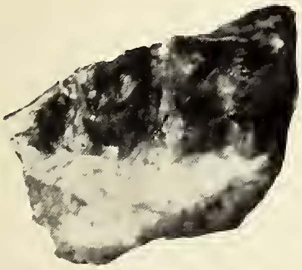

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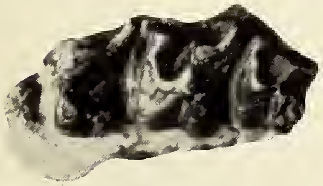

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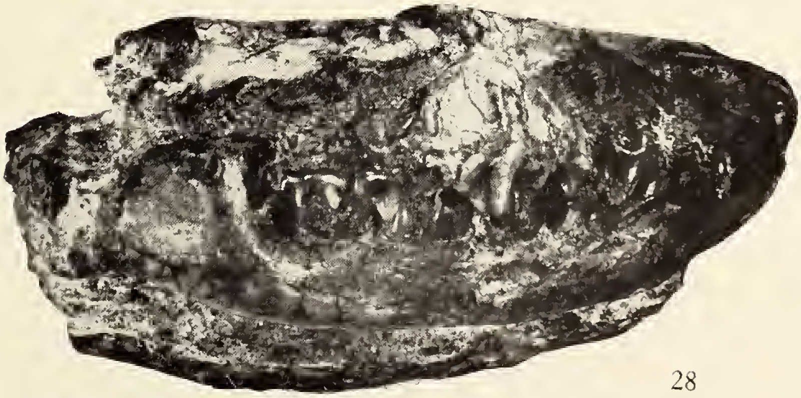

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AMPHECHINUS, NEUROGYMNURUS, GYMNURECHINUS & GALERIX

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